Author:
Chapman, Katherine E

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Impacts of motorboat noise on the parental-care behaviours of two species of coral-reef damselfish (Pomacentridae).

Impacts of motorboat noise on the parental-care behaviours of two species of coral-reef damselfish (Pomacentridae).

Katherine Elizabeth Chapman

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Abstract

Anthropogenic noise-pollution from human activities, such as construction, oil exploration, and vessel traffic, is a growing threat to marine environments. A range of noise-induced effects on the physiology and behaviour of fish are known, but only a few studies have investigated the effects of noise on behaviours with a direct relationship to fitness, such as parental care. Furthermore, most research has tested the responses of captive fish using short-term playback of noise recordings. More evidence is required regarding impacts of noise directly from the source in natural conditions, and on long-term effects from repeated exposures. The current study investigated the impacts of short-term and long-term (repeated) exposure to motorboats on the parental-care behaviours of two species of coral-reef damselfish (family Pomacentridae). Short-term motorboat-noise exposure caused Ambon damselfish *Pomacentrus amboinensis* to reduce egg tending in favour of increased vigilance compared to an ambient-sound control. Long-term repeated motorboat exposure did not cause spiny pullers *Acanthochromis polyacanthus* to change their baseline larval-defence behaviours. However, short-term noise did cause a temporary increase in anti-intruder display rate, and the parents showed sensitisation in this response over the course of a month-long exposure regime, compared to ambient-sound control nests. Impacts of motorboat noise on the parental-care behaviours of fish could lead to reduced survival or compromised development of offspring, so decrease reproductive success. It is therefore important that policymakers and motorboat users are presented with comprehensive evidence of the real-world effects of motorboat noise in order to develop effective mitigation strategies. More evidence is required on the long-term effects of repeated and chronic anthropogenic noise on fish to best inform practice, particularly in relation to fitness-influencing behaviours.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: DATE:

Table of contents

List of figures and tables

CHAPTER ONE

A review of the effects of anthropogenic noise in the ocean on fish physiology and behaviour.

1.1 Literature review

1.1.1 Anthropogenic noise

Anthropogenic noise can be defined as sounds produced by human activity which contain minimal useful information and are detrimental to the organisms which detect them, and is recognised by the United Nations as a global pollutant. It is rapidly increasing in distribution and intensity in both terrestrial and marine environments. Sources of noise pollution in the oceans include military activities, construction, seismic surveying, oil exploration and vessel traffic (review: Hildebrand 2009). These sources may produce impulsive or prolonged noise at a broad range of frequencies and intensities (Francis and Barber 2013), which, due to the physical properties of sound waves underwater, can propagate over great distances (Pine et al. 2016). Consequently, anthropogenic noise is now a dominant feature of marine soundscapes.

One of the most widespread and prevalent sources of human noise in the oceans is vessel traffic; cargo, fishing, transport and recreational vessels contribute to the huge global fleet. More than 50,000 cargo ships and 4.6 million fishing vessels are active worldwide (FAO 2019; ICS 2019), and over 11 million engine-driven recreational vessels are registered in the USA alone (U.S. DHS et al. 2016). Productive, attractive coastal habitats such as coral reefs are particularly vulnerable to the increasing pressures of noise pollution from human exploitation and recreational activities (Pine et al. 2016); the Great Barrier Reef is expected to host half a million recreational boats by 2040 (GBRMPA 2014).

There is an increasing awareness of the detrimental effects of noise pollution on organisms; a large body of evidence already exists detailing a variety of impacts on a range of terrestrial and marine taxa (reviews: Gill et al. 2015; Kunc et al. 2016; Shannon et al. 2016). Animals can suffer direct injury if exposed to excessively high intensities of impulsive noise, such as damage to hair cells from airgun explosions for oil exploration (McCauley et al. 2003). Less sudden but potentially equally severe effects are those affecting the development, physiology and behaviour of animals, which come about through three main mechanisms. First, noise can cause responses typically associated with stress in both invertebrates and vertebrates (Wright et al. 2007; Wale et al. 2013; Vazzana et al. 2017). These physiological changes tend to occur rapidly after the onset of noise and could impact individual survival via condition deterioration or disrupted development (Santos et al. 2010; Fakan and McCormick 2019). Second, noise may be a source of distraction from natural stimuli; behaviours may be performed with reduced efficiency or not exhibited at all during exposure, and important environmental and social cues and signals could be ignored (Chan et al. 2010; Purser and Radford 2011). Finally, if artificial noise in an environment occurs at similar frequencies to biologically important sounds, cues and signals can be masked and the recipient unable to perceive them

effectively (Vasconcelos et al. 2007; Holles et al. 2013; Pine et al. 2016). Signal masking is expected to have stronger effects when the spectral composition of the noise covers the peak frequency sensitivities of the animal, as these sensitivities will most likely coincide with conspecific acoustic communication frequencies (Codarin et al. 2009; Ladich 2013).

Stress, distraction and masking have wide-ranging impacts on animals across ecological scales. At the individual level, for example, boat-noise playback disrupted the orientation of larval flame cardinal fish *Apogon doryssa* to reef noise (Holles et al. 2013), and the settlement behaviour of larval corals *Pocillopora damicornis* and *Acropora cytherea* (Lecchini et al. 2018). Noise has also been shown to impact social behaviours including shoaling; for instance, European seabass *Dicentrarchus labrax* exhibited reduced cohesion, coordination and directionality of group movements during pile-driving playback (Herbert-Read et al. 2017). Furthermore, there can be disturbance to interspecific interactions, such as cooperation. During exposure to real motorboat passes, cleaner wrasse *Labroides dimidiatus* increased the time spent inspecting clients before engaging in cleaning, and cheated more often by biting clients, but received punishment less often in response (Nedelec et al. 2017b). At the community scale, Paxton et al. (2017) observed a 78% decline in abundance over all fish species on a reef whilst seismic surveying occurred 8 km away.

While it is known that anthropogenic noise can adversely affect many marine taxa, including corals (Lecchini et al. 2018), molluscs (de Soto et al. 2013; Nedelec et al. 2014), crustaceans (Chan et al. 2010; Wale et al. 2013) and mammals (Tyack et al. 2011), much of the recent literature has focused on fish. Many fishes have good hearing, and use acoustic cues and signals for a variety of behaviours, such as orientation (Simpson et al. 2010; Radford et al. 2011; Parmentier et al. 2015), courtship (Kenyon 1994; Lobel and Mann 1995; Mann and Lobel 1998) and territory defence (Myrberg 1997; Sebastianutto et al. 2011), and as such are vulnerable to noise pollution. It is important to understand the impacts of noise on fish, as they have vital ecosystem roles including as grazers, intermediary consumers, predators and prey (Lewis 1986; Kozlov 1995; Mumby et al. 2006; Cole et al. 2008). Furthermore, fish are central to the health and wellbeing of humans, as they are a key protein source for over 3 billion people worldwide, and over 56 million people are employed directly in the fishing and aquaculture industries (FAO 2016).

1.1.2 Physiology and development

Many studies have investigated the effects of anthropogenic noise on secondary indicators of stress in fish, particularly oxygen consumption, ventilation rate and heart rate. The Ambon damselfish

Pomacentrus amboinensis showed increased oxygen consumption within a short period of time after the onset of motorboat noise in both laboratory playback trials and in field trials with real motorboats (Simpson et al. 2016b). Similarly, embryonic clownfish *Amphiprion spp.* had higher heart rates during tonal-noise exposure (Simpson et al. 2005); heart-rate increases have also been recorded in embryonic staghorn damselfish *Amblyglyphidodon curacao* exposed to real boats (Jain-Schlaepfer et al. 2018). Additionally, stress responses to anthropogenic noise have been measured in fish using haematological factors such as hormones in blood plasma (Crovo et al. 2015; Celi et al. 2016; Vazzana et al. 2017). Negative impacts of stress may include deterioration of body condition, failure to perform behaviours efficiently or altered decision making (review: Schreck et al. 1997). The physical condition of individuals may impact the severity of the stress anthropogenic noise causes: European eel *Anguilla anguilla* juveniles in poor condition had increased ventilation rates during playback of ship noise but those in good condition showed no such response (Purser et al. 2016). This suggests that noise effects could interact with natural fluctuations in body condition to influence individual survival; for example, resulting in greater mortality following the breeding season when condition tends to be poorer (Chellappa et al. 2003; Kortet et al. 2003).

Juvenile development may be affected by noise: motorboat-noise playback caused eggs of the spiny chromis *Acanthochromis polyacanthus* to have smaller yolks, which could potentially decrease larval survival post-hatching, and larvae exposed to noise as embryos had altered morphologies compared to those exposed to ambient-sound controls (Fakan and McCormick 2019). However, no such effects were found in the same study for embryonic cinnamon clownfish *Amphiprion melanopus,* and no effect of motorboat-noise playback on hatching, survival or growth of daffodil cichlid *Neolamprologus pulcher* eggs was found by Bruintjes and Radford (2014).

1.1.3 Foraging behaviours

Foraging efficiency may affect individual condition, predation risk and breeding success (Cerri and Fraser 1983; Abrahams 1993; Wenger et al. 2012). Disruption of typical foraging regimes in the Mediterranean chromis *Chromis chromis* in areas with high recreational boating activity led to poor body condition (Bracciali et al. 2012). These fish were behaviourally flexible, shifting their feeding patterns away from peak boating times towards dawn and dusk, although this resulted in reduced intake, presumably as the prey were harder to see. Additionally, these fish attempted energy intensive escape responses from the boat noise. Playback of white noise has been shown to distract three-spined sticklebacks *Gasterosteus aculeatus*, which exhibited increased handling errors and impaired discrimination between food and non-food items compared to fish in a silent control treatment

(Purser and Radford 2011); zebrafish *Danio rerio* showed a similar reduction in foraging efficiency when exposed to artificial noise (Shafiei Sabet et al. 2015). European minnows *Phoxinus phoxinus* consumed fewer prey items during exposure to playback of harbour noise with a ship passing versus harbour noise only, due to a behavioural shift towards inactivity or sociality, rather than reduced efficiency *per se* (Voellmy et al. 2014a). Changes in the foraging activities of fish could impact nutrient cycles and ecosystem productivity via trophic cascades (Francis and Côté 2018). Furthermore, fishes may change their reproductive output depending on food availability (Tyler and Stanton 1995), in which case noise-induced changes to foraging may indirectly influence reproduction.

1.1.4 Risk assessment, anti-predator behaviours and territoriality

Risk assessment during decision making, escape responses from predators and predator-deterrent behaviours have obvious implications for survival (Cerri and Fraser 1983; Krause and Godin 1996; Mirza and Chivers 2000; Lönnstedt et al. 2012; Goiran and Shine 2015). Additionally, compromised territorial behaviours, particularly against conspecifics, could result in the loss of a high-quality territory, affecting future reproductive success (Hourigan 1986).

Fish can alter their behaviour relative to the assessed risk of an action at any given time, and noise could impact risk via changes to predator abundance or behaviour, or from masking environmental cues or conspecific signals. The noise or noise source itself could also be perceived as a threat. Ward's damselfish *Pomacentrus wardi* reduced bold behaviours in real boat noise, an appropriate response to increased threat level, however failed to respond appropriately to conspecific alarm pheromones (McCormick et al. 2018), suggesting that boat noise can affect sensory modalities differently. It may be that the fish categorised the noise as a threat to shelter from, whereas the chemical cue was misinterpreted, perhaps due to distraction. Another explanation for reduced risk-taking could be that the individual is compensating for its reduced ability to correctly recognise and respond correctly to environmental cues as a result of masking or distraction (McCormick et al. 2018). Similarly, red-mouthed goby *Gobius cruentatus* exposed to playback from small motorboats spent more time under shelter and less time stationary in the open, which suggests a perceived increase in threat (Picciulin et al. 2010), which was also true for European seabass exposed to drilling or pile-driving playback (Spiga et al. 2017). Sharks also appear to have a risk-averse response to noise; fewer individuals were observed around a baited rig exposed to continuous artificial noise, with higher latency to approach and fewer interactions with the rig compared to a silent control treatment across seven coastal and reef species (Chapuis et al. 2019). Since similar responses were found to playback

of orca *Orcinus orca* calls, a known predator of sharks, these results imply increased threat perception (Chapuis et al. 2019).

The ability of prey species to detect, identify, avoid and escape potential predators could be hindered by anthropogenic noise, having a direct impact on individual survival. A stressed or distracted individual could miss a cue, compromising their ability to respond to the threat in sufficient time, if at all. Important behavioural trade-offs, for example between foraging and threat responses, could be influenced, since individuals spending more time on risk-avoidance inevitably have less time for other behaviours.

The likelihood of a startle response occurring and the speed of the response were reduced in European eels subjected to a looming stimulus during ship-noise playback compared to an ambient-sound control (Simpson et al. 2015). Slower responses to threatening stimuli could allow a predator to get closer before eliciting an escape response from the target, potentially increasing prey mortality rates. This was demonstrated in the Ambon damselfish, which responded poorly to predator stimulation when exposed to noise from small motorboats; juveniles were six times less likely to respond to a looming stimulus in noise than in ambient conditions, and when responses occurred, they were 20% slower (Simpson et al. 2016b). These results were repeatable in the field with real motorboats, where 2.4 times as many individuals were captured by dusky dottybacks *Pseudochromis fuscus* compared to in ambient conditions. Multimodal disruption of anti-predator behaviours has also been demonstrated in fish: the fathead minnow *Pimephales promelas* failed to startle in response to conspecific olfactory alarm cues when exposed to motorboat-noise playback in tanks (Hasan et al. 2018); a similar cross-modal result as was found by McCormick et al. (2018). Noise exposure during predator-recognition learning was also detrimental to the survival of Ambon damselfish, as larvae played recorded boat noise failed to learn how to recognise predators or associate conspecific alarm pheromones with visual threat cues (Ferrari et al. 2018). However, these effects on escape behaviours are not always found. The European minnow showed no effect of playback on latency to startle under ship-noise playback (Voellmy et al. 2014b), highlighting the potential for interspecific variation in responses to noise and the importance of species-specific studies. Noise-induced disruption to anti-predator behaviours, particularly during vulnerable life-history stages, could lead to decreased survival of larvae and adults, and more occurrences of low larval-recruitment seasons as anthropogenic noise in the oceans intensifies.

Deterrence of territorial intruders is known to be influenced by noise pollution in some fish. Red-mouthed goby had a reduced success in expelling conspecific intruders from their territory when exposed to motorboat-noise playback as opposed to a silent control in tank conditions, most likely

due to masking or disruption of defensive acoustics (Sebastianutto et al. 2011). This could result in the loss of a high-quality territory to conspecifics or other space-competitors. Compromised territorial defence against predators during noise exposure has also been found in the daffodil cichlid, where females decreased anti-predator behaviours under boat-noise playback (Bruintjes and Radford 2013), and the spiny chromis (Nedelec et al. 2017a), both discussed below in the context of offspring defence.

1.1.5 Reproduction

There are few studies which explicitly measure the impact of anthropogenic noise on reproductive success in fish, despite the significance of such measures to fitness. Negative impacts on breeding behaviour were found in the common goby *Pomatoschistus microps* when exposed to continuous playback of boat-mimicking frequencies versus intermittent playback or an ambient-sound control in tanks: the latency to nest inspection by a female and the latency to spawn increased, and the likelihood of spawning decreased (Blom et al. 2019). Noise can mask the cues and signals used by fish to mediate breeding behaviours. Acoustic spectra from ferry engines coincided with the peak frequency sensitivity of the Lusitanian toadfish *Halobatrachus didactylus*, the males of which vocalise to attract females and deter rival males, causing an increase in the auditory threshold (Vasconcelos et al. 2007). This reduced the perception distance for vocalisations, which could potentially decrease male mating success rate (Vasconcelos et al. 2007). Other fish affected by threshold changes in conspecific signal-reception in the presence of boat noise include Mediterranean chromis*,* brown meagres *Sciaena umbra* and red-mouthed gobies (Codarin et al. 2009). The painted goby *Pomatoschistus pictus* also experienced signalling disruption in noise: this fish reduced acoustic and visual reproductive signals when exposed to continuous low-frequency noise mimicking a small boat engine and spawning likelihood fell compared to fish not subjected to noise (de Jong et al. 2018).

1.1.6 Parental care

Evidence of the indirect effects of noise exposure on the growth and survival of offspring via effects on parental behaviours is limited. The effects on anti-predator behaviour in fish discussed above can impact nest success, as parents with disrupted anti-predator responses may suffer a higher loss of offspring to predation (Nakazono 1993). In addition, noise could alter the condition of the parent (Bracciali et al. 2012) and so disrupt behavioural trade-offs with foraging (Nedelec et al. 2017a). Impacts on parental care can alter individual breeding success (Gross 2005) therefore could lead to a population level decline in recruitment.

Eighty-nine families of teleost fish exhibit parental care (Blumer 1982), which in externally fertilising fish includes behaviours such as nest maintenance (Hale and St Mary 2007), egg tending (Zoran and Ward 1983), food provisioning (Buckley et al. 2011) and defence against predators and nest-site competitors (Haley and Müller 2002). In external fertilisers, brood care is commonly performed by individual males, which have lower fertility costs when providing care than females relative to the benefits of increased juvenile survival (Gross and Sargent 1985); in some species, biparental care has also evolved where females gained a survival advantage from the safety of a territory (Gross and Sargent 1985), and some fish exhibit female-only care or cooperative-kin care (Taborsky 1984). Territoriality is beneficial to males as it increases the certainty of paternity of a clutch (Werren et al. 1980), and although territoriality and egg or larval care is energetically costly, males can counterbalance these costs by continuing to mate during the care period, increasing their lifetime reproductive output (Gross and Sargent 1985; Magrath and Komdeur 2003).

Boat-noise playback affected the parental-care behaviours of the daffodil cichlid (Bruintjes and Radford 2013). This fish has a cooperative breeding system in which nest digging and anti-predator behaviours are performed by a dominant breeding pair and subordinates. Nest-digging rate and anti-predator behaviours decreased during noise playback compared to a silent track. Additionally, dominant–subordinate interactions were altered. However, the anti-predator behavioural response was dependent on the presence of eggs: with eggs present, there was no decline in rate at the onset of noise. It may be that even if fish are compromised in their breeding behaviour by noise, the effects of noise are alleviated once eggs are present, perhaps due to the higher cost of poor care in this context. This study additionally found a sex-specific effect in the responses, with males reducing nest maintenance whilst females reduced defence, emphasising the potential for complex intraspecific responses to noise.

No effects of motorboat-noise playback were found on the parental-care behaviours of egg-tending male largemouth bass *Micropterus salmoides* (Maxwell et al. 2018). This was true for three types of engine noise: combustion engine at high speed, combustion engine idling and an electric tolling motor. The time spent on the nest, the number of fin beats and the number of turns made by the male – a proxy for vigilance – were all unaffected. However, motorboat noise did have a significant effect on the turning behaviour once the larvae had hatched, indicating a context-dependent result to complement that found by Bruintjes and Radford (2013). The largemouth bass experiment only exposed the fish to noise for 1 min, which may not have been enough time to capture changes in behaviour during the egg phase.

Like other behavioural responses, parental-care behaviours may not be instantly affected by noise exposure but may be altered over time. In boat-noise-playback experiments by Picciulin et al. (2010), the Mediterranean damselfish showed no response to noise initially, but in the longer term reduced the time spent on egg tending and nest maintenance compared to fish in the natural ambient-sound conditions of the site. This study suggests that only investigating short-term responses to noise, as most of the anthropogenic-noise literature does, overlooks chronic-exposure effects.

Addressing this gap, Nedelec et al. (2017a) investigated the effects of 12 days of intermittent motorboat-noise playback on spiny chromis parents at natural nests. Six of 19 noise-treatment nests exhibited complete offspring mortality after 12 days, despite parents in the noise treatment doubling the frequency of territorial behaviours compared to the ambient-sound playback treatment, in which no instances of complete mortality occurred. There was also a reduction in glancing (mucus feeding by the offspring from a parent; Kavanagh, 1998), however there was no effect on offspring growth. The increased defence resulted in a temporal trade-off with foraging, which decreased by 25%; this could affect the condition and therefore the future reproductive opportunity of the adult. However, over the course of the long-term exposure in these fish, feeding time increased again; perhaps the initial decrease was instead due to distraction rather than a trade-off with defence. The authors suggest that stress-induced aggression could explain the increase in defence, whereas distraction could have caused parents to attack inappropriately or with low efficiency, hence the higher offspring mortality.

1.1.7 Recovery and compensation

Some species have been shown to recover rapidly from the negative impacts of short-term noise after exposure ceases and to habituate to repeated exposures in the long term. Immediately following the end of short-term exposure to ship-noise playback, both European eels and European seabass rapidly recovered normal ventilation rate, which had increased during noise playback versus an ambient-sound control (Bruintjes et al. 2016). This indicates that stress in these species does not persist beyond the exposure period. After a 12-week exposure to seismic-survey or pile-driving playback, captive European seabass showed no response in ventilation rate, having initially shown an increased rate compared to fish exposed to ambient-sound playback, and did not show any response to subsequent short-term exposures (Radford et al. 2016). The same species increased swimming speed and depth when initially exposed to impulsive noise, but changed depth less following repeated exposures: this reduction in effect was seen over only two days, and could be interpreted as desensitisation or habituation (Neo et al. 2018).

An even shorter recovery was found in the behaviour of Ambon damselfish juveniles, which immediately reduced levels of boldness – e.g. time spent at certain distances from a shelter – at the onset of motorboat-engine noise in field conditions, but recovered normal behaviour after only 20 minutes of continuous exposure (Holmes et al. 2017). Boldness relates to survival through susceptibility to predation (McCormick and Meekan 2010), so this ability to desensitise to boat noise would be beneficial at this vulnerable life-history stage. A similar recovery was seen after long-term exposure in the domino damsel *Dascyllus trimaculatus*: while naïve fish responded to intermittent motorboat-noise playback with increased ventilation rate and increased sheltering in comparison with an ambient-sound control, no effects of noise input were seen after two weeks of exposure (Nedelec et al. 2016b).

Some species have the potential to compensate for masking effects, such as by signal-component alteration, signal redundancy and modality shifts, as well as simply avoiding the noise source, although the latter would be limited in territorial species or where anthropogenic activity is widespread (Radford et al. 2014). Brown meagres increased the mean pulse rate of their courtship calls in response to long-term repeated exposure to real boat noise (Picciulin et al. 2012). The painted goby shifted signalling modality preference towards reliance on visual signals when continuously exposed to low-frequency noise, which led to a relative increase in spawning likelihood in acoustically disturbed conditions (de Jong et al. 2018). For species demonstrating signalling plasticity, the negative effects of masking may be less severe, or avoided entirely.

Evidence of fish demonstrating both recovery from and plastic responses to anthropogenic noise gives us a positive outlook regarding the predicted increases in the numbers and distributions of noise sources. It is possible that some species will be able to cope with noise without requiring mitigation, and some may simply not be affected in the long term.

1.1.8 Concluding remarks

The current literature provides evidence of anthropogenic noise pollution disrupting a range of physiological and behavioural traits in fish. However, the majority of studies focus at the individual level, and are largely conducted in tanks, with short-term playback of recorded noise. Although a handful of experiments have explored effects in natural conditions, with longer exposures, and/or with real noise sources, this field must continue to expand by addressing these elements. More work regarding repeated-exposure and chronic-exposure effects – the potential for long-term recovery, habituation and adaptive compensation – and predictive long-term impact modelling at community

and ecological scales would be particularly beneficial. It would be interesting to explore how historical exposure affects behaviour and survival later in life, and whether generational carry-over effects occur. An increase in *in situ* experiments with real noise sources would be most informative, as this would provide clearer evidence of the real-world effects of anthropogenic noise, usable by policymakers and stakeholders in the design of effective mitigation strategies. Furthermore, it would be beneficial to shift the focus to population, community and ecological effects, which will better inform mitigation at a realistic scale. This could be partially addressed by extrapolating from evidence of effects on reproduction and breeding behaviours, such as parental-care behaviours, which are currently poorly studied.

Motorboat noise is an especially common, widespread source of noise in marine habitats, and playback studies using motorboat noise make up a large proportion of the recent anthropogenic noise literature. Motorboat-noise intensity is easily manipulated (e.g. by driving more slowly or further from habitats), therefore is a key target for simple, inexpensive pollution mitigation (McCloskey et al. in preparation). However, playback of recorded noise does not accurately reproduce the acoustic properties of noise directly from the source, so there is a need for studies to investigate impacts on organisms from real boats. This will provide evidence which can be interpreted more reliably in terms of real-world populations in order to better inform relevant mitigation strategies.

1.2 Thesis aims

To test the hypothesis that motorboat-noise exposure compromises the parental-care behaviours of brooding fish, I investigated responses in two species of common Indo-Pacific coral-reef damselfish (family Pomacentridae): the Ambon damselfish *Pomacentrus amboinensis* and the spiny chromis *Acanthochromis polyacanthus* (Kavanagh 2000; Emslie and Jones 2001). These species are highly territorial and exhibit site-fidelity over small home ranges, a common trait among pomacentrids (Petersen 1995; Kavanagh 2000; McCormick and Meekan 2007). Both species have been shown to be disturbed by motorboat noise previously (Simpson et al. 2016b; Nedelec et al. 2017a; McCormick et al. 2018).

Pomacentrus amboinensis exhibits male-only parental care of demersal clutches of eggs within a nest during the breeding season (October–January) (McCormick and Meekan 2007); the eggs hatch approximately 4 days after spawning (Kerrigan 1997; Emslie and Jones 2001). Since this species is polygamous (Fishelson 1998) and males continue to mate during the brooding period, nests often contain multiple clutches of different ages from more than one female. Egg tending mainly involves

fanning clutches with the pectoral and dorsal fins to oxygenate the developing embryos (Moyer, 1975; McCormick and Smith, 2004; McCormick and Meekan, 2007).

Acanthochromis polyacanthus exhibits biparental care of larvae, guarding the offspring from potential predators throughout the breeding season (October–February) (Robertson 1973). This species is unusual in having no pelagic larval stage; a single brood of fry live within the parental territory for up to 4 months post-hatching, after which the fry gradually dissociate from the area (Kavanagh 2000). Remaining on the reef as larvae greatly increases the risk of predation, therefore the larvae are reliant on the territorial behaviours of the parents for survival (Thresher 1985).

For this thesis, egg-tending male *P. amboinensis* were exposed to short-term motorboat noise (Chapter 2), and larvae-guarding pairs of *A. polyacanthus* were exposed to both short-term and repeated long-term motorboat noise (Chapter 3) in natural conditions. Both experiments were conducted on populations of wild, free-swimming fish, and used real motorboats as the source of noise, to progress beyond the typical tank-based and/or playback experiments currently dominating the literature.

1.3 Ethics statement

These experiments adhered to the legal requirements of the country in which they were conducted (Australia) in strict accordance with the guidelines of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (8th Edition 2013). Permits were granted by the Great Barrier Reef Marine Park Authority and the Queensland Parks and Wildlife Service (Permit G17/39752.1) and the Queensland Department of Agriculture Fisheries and Forestry (Permit 170251). Ethics approval for both fieldwork seasons at Lizard Island Research Station was granted by James Cook University Animal Ethics Committee (Application A2361), the University of Exeter (Application 2013/247) and the University of Bristol Animal Welfare Ethical Review Board (University Investigator Number UB/16/057).

CHAPTER TWO

Motorboat noise impacts the egg-tending behaviours of a coral-reef fish, *Pomacentrus amboinensis.*

Chapter contributions:

Experimental design –

Katherine E. Chapman (lead), Andrew N. Radford, Stephen D. Simpson, Lucille Chapuis, Kieran P. McCloskey.

Fieldwork –

KEC (lead), LC, KPM.

Video and statistical analysis and write-up –

KEC.

2.1 Abstract

Noise pollution from human activity is growing in distribution and intensity in marine environments, and is known to have a detrimental effect on the physiology and behaviour of a variety of taxa. However, there is relatively little evidence regarding the effects of noise on behaviours with direct links to fitness, particularly in wild populations. Here, wild brooding males of the common coral-reef fish *Pomacentrus amboinensis* were exposed to noise from small motorboats, to investigate the effects of this stressor on parental egg-care behaviours. These fish reduced the percentage of time in the nest spent on egg tending and increased the percentage of time spent on vigilance during short-term noise exposure. Consequently, the development and/or hatching success of the eggs may be adversely impacted by anthropogenic noise via effects on the care-providing parent.

2.2 Introduction

Anthropogenic noise is a widespread and increasing global pollutant which is prevalent in marine habitats, particularly along coastlines. Sources of marine noise pollution include construction, military activities, seismic surveying and vessel traffic (review: Hildebrand 2009). A range of effects of anthropogenic noise on animals is already evidenced across taxa (reviews: Gill et al. 2015; Kunc et al. 2016; Shannon et al. 2016). The most concerning impacts of noise are those which have direct links to fitness, such as disrupted development (Nedelec et al. 2014), reduction in anti-predator responses (Simpson et al. 2016b; McCormick et al. 2018) and decreased breeding success (Nedelec et al. 2017a; de Jong et al. 2018) as these can lead to population- and ecosystem-level consequences.

There is a growing body of evidence concerning the effects of anthropogenic noise on fish development, physiology and behaviour. For example, motorboat-noise playback disrupted the development of spiny chromis *Acanthochromis polyacanthus* embryos, which had smaller yolks and abnormal larval morphology compared to those in ambient conditions (Fakan and McCormick 2019). Ferry-engine noise masked the reproductive acoustic communication of the Lusitanian toadfish *Halobatrachus didactylus*, which could lead to decreased mating success (Vasconcelos et al. 2007). Behavioural responses to noise have been found in the European seabass *Dicentrarchus labrax* which increased vigilance, exploration and sheltering when exposed to drilling or pile-driving playback (Spiga et al. 2017), and motorboat noise compromised the anti-predator startle response of Ambon damselfish *Pomacentrus amboinensis* larvae, resulting in higher mortality (Simpson et al. 2016b). These illustrative examples are among many demonstrating a variety of changes in fish caused by noise which could influence individual fitness. However, only a handful of studies have explored the impacts of anthropogenic noise on parental-care behaviours in fish.

Eighty-nine families of teleost fish exhibit some level of parental care (Blumer 1982). Parental care comprises a suite of behaviours, including nest maintenance, egg tending, food provisioning, and defence against competitors and predators (Zoran and Ward 1983; Haley and Müller 2002; Hale and St Mary 2007; Buckley et al. 2011), which directly influence offspring survival and therefore fitness. Bruintjes and Radford (2013) found that captive male daffodil cichlids *Neolamprologus pulcher* reduced nest-digging rate and delayed starting this behaviour during exposure to motorboat-noise playback, as well as reducing anti-predator behaviours, but only when there were no eggs in the nest. Similarly, Picciulin et al. (2010) found a negative effect of boat-noise playback on the time Mediterranean chromis *Chromis chromis* spent nest cleaning and egg tending at natural nests. More recently, Nedelec et al. (2017a) showed an increase in nest-defence behaviours but higher offspring mortality in spiny chromis parents experiencing 12 days of motorboat-noise playback at natural nests

during the larval stage. The direct fitness consequences of parental care make these behaviours an obvious, but largely neglected, target for study in relation to anthropogenic noise.

This study aimed to further our understanding of how parental-care behaviours are influenced by anthropogenic noise with an *in-situ* experiment on the effects of a real noise source (motorboats) in a population of free-swimming fish. Coral reefs are exposed to high levels of vessel traffic from shipping, fishing, transport and recreation (Holles et al. 2013); it is timely to investigate noise pollution in these vulnerable ecosystems to inform mitigation measures. The Ambon damselfish *Pomacentrus amboinensis* is an abundant Indo-Pacific coral-reef damselfish (family Pomacentridae) (Emslie and Jones 2001). This species has previously been shown to be disturbed by motorboat noise, notably in assessment of risk (McCormick et al. 2018), predator-recognition learning (Ferrari et al. 2018), anti-predator behaviours (Simpson et al. 2016b), and feeding and movement (Holmes et al. 2017). *P. amboinensis* is polygamous (McCormick and Smith 2004) and exhibits male-only parental care of demersal clutches of eggs within an aggressively-guarded nest during the breeding season (McCormick and Meekan 2007). During egg tending, males guard their territory from intruders and egg predators, maintain the nest, clean the clutch and oxygenate the eggs by fanning with their pectoral and dorsal fins (Moyer 1975; McCormick and Smith 2004; McCormick and Meekan 2007). Previous work has shown that this species readily occupies artificial nests such as terracotta tiles (Kerrigan 1997) or PVC half-pipes (Emslie and Jones 2001) in the wild. In addition to their high site-fidelity and small home-ranges, this makes breeding males easy to manipulate experimentally, giving an insight into the behaviours occurring inside and immediately around the nest.

In this study, I tested responses in the within-nest parental-care behaviours of egg-tending *P. amboinensis* to engine noise from small motorboats. I aimed to determine whether key behaviours with direct consequences for egg growth and survival are detrimentally affected by exposure to motorboat noise compared to ambient sound, to test the hypothesis that noise-exposed *P. amboinensis* males are less attentive parents.

2.3 Methods

2.3.1 Field methods

From October to December 2018, I recorded videos of individual free-swimming *P. amboinensis* males guarding broods of eggs within artificial nests at Lizard Island Research Station, Queensland, Australia (14°4´S 145°28´E), with and without motorboats driving nearby.

I worked at six 100-metre-long sites, a minimum of 100 m apart, in the lagoon area to the south of Lizard Island; a shallow (~0.5–10 m deep), sheltered area of degraded coral reef. I placed between 20 and 30 identical PVC half-pipes (30 cm length, 18 cm diameter) on the sandy sediment along the edges of the reef at each site to act as artificial nests, allowing for easy observation and manipulation (McCormick and Meekan 2007). These nests were explored and subsequently occupied by individual male *P. amboinensis* within minutes of placement. The distance between each nest was determined by the natural proximity of the males; half-pipes were placed near relatively large individuals observed to exhibit territorial aggression, to increase the likelihood of attracting adults. Eggs were laid by visiting females on the underside of the nest, which could be lifted to monitor egg presence; the resident male rapidly re-entered following this disturbance. If a nest was found to be unoccupied, it was moved to another location at the same site, near to a different male. Occupation was tested by closely approaching an unattended nest and touching it; temporarily absent resident males rapidly returned to the nest and responded aggressively to this motion. I monitored each site approximately every 2–3 days in rotation and ran experimental trials within two days of eggs being found, as the incubation period for a single clutch in this species is only around four days (Kerrigan 1997).

Egg-tending behaviours occurring within the nest were recorded twice for each nest on the same day, with one motorboat-noise trial and one ambient-sound control trial; the trial order was randomly assigned each day. I filmed multiple nests simultaneously, using weighted GoPro Hero 5 cameras set approximately 10 cm from the entrance to the nest by a snorkeler who then left the area. In both treatments, I waited 5 min to allow the fish to resume normal behaviour following this disturbance (Nedelec et al. 2016b), before recording behaviour for 10 min to determine baseline levels in ambient-sound conditions. In the motorboat-noise trials, the nests were then exposed to a 5-m long motorboat (30 horsepower 4-stroke outboard motor) driven continuously at full speed for 10 min in the vicinity of the site, approximately 10 m from the reef edge. Five boats were used over the course of the experiment to minimise pseudoreplication of the noise source. For control trials, I continued to record behaviour in ambient-sound conditions for 10 min following the baseline period; throughout control trials, the motorboat remained anchored 20 m away from the reef to reduce the chance the fish might detect noise from waves hitting the boat. To minimise the likelihood of carry-over effects from motorboat-noise exposure, I left two days between pairs of trials at the same site or at adjacent sites. I collected videos at 38 nests over 11 non-consecutive days.

2.3.2 Acoustic characterisations

To characterise the sound treatments acoustically, recordings of ambient-sound conditions and motorboat-noise conditions were made at the six study sites in December 2018, using three of the motorboats and the same driving regime as in the experiment. A triaxial accelerometer with integrated hydrophone (M20-040; Geospectrum Technologies, Dartmouth, Canada) and a digital track recorder (F8 field recorder, sampling rate 48 kHz; Zoom Corporation) were deployed at the approximate half-way point of each site at approximately 1.5–2.5 m depth, so that particle motion and acoustic pressure were both recorded.

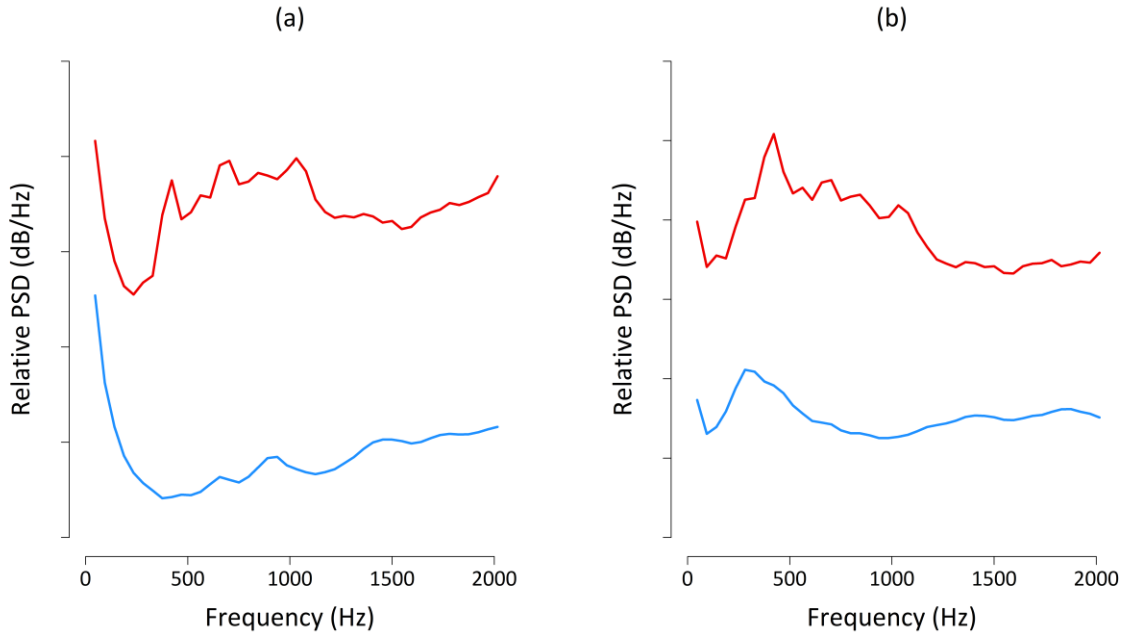

Figure 2.1: Relative power spectral density (PSD) plots for (a) particle motion and (b) acoustic pressure for frequencies <2000 Hz over 1-min tracks for the two sound treatments used in the experiment (average of four 60 s samples per sound treatment, window length = 1024, overlap = 50%, sample rate = 48 kHz). Y-axis ticks at 10 dB /Hz intervals. Red line shows relative PSD for the averaged motorboat-noise treatment (combined recordings from three boats at four sites); blue line shows relative PSD for the averaged ambient-sound treatment (combined recordings from four sites).

Recordings from two sites were removed from the analysis due to acoustic artefacts and interference. Tracks were analysed in MatLab 2013a (MathWorks, Natick, MA, USA) using *paPAM* (v0.872: Nedelec et al. 2016a). Power spectral densities (PSDs; Figure 2.1) were calculated from 'averaged' 1-min tracks with a window length of 1024, and a window overlap of 50%, with a low-pass filter at 2 kHz to focus on frequencies which are of most relevance to typical fish hearing (Wright et al. 2005). The tracks consisted of combined samples of recordings from three motorboats at four sites or samples of ambient-sound conditions at four sites stitched into one 1-min track per sound treatment. Owing to technical issues – physical damage to the recording equipment resulting in excessive noise in one channel – PSD plots comparing the two sound treatments are presented with uncalibrated particle-motion and acoustic-pressure values. This characterisation illustrates the relative difference between the two treatments, showing that the motorboat-noise treatment had greater particle motion and acoustic pressure compared to the ambient-sound control treatment across all frequencies. This analysis is sufficient for this study, as hearing sensitivities and masking effects comparing the treatments to the acoustics of the fish were not investigated.

2.3.3 Behavioural data extraction

Videos were cropped to the baseline (ambient sound) and treatment (ambient sound or motorboat noise) periods using ffmpeg (open source: ffmpeg.org). Two nests were removed from the study due to unusable camera angles, and two more were removed due to filming of non-focal species occupying the nests, which had been incorrectly identified in the field.

The cropped videos were saved with coded file names by a colleague and were watched with no sound so that I was blind to the sound treatments and period. Using the behavioural observation software BORIS (Friard and Gamba 2016), I extracted data on within-nest behaviours: nest visits, egg fanning, nest maintenance and vigilance (Table 2.1). I approximated the duration of dorsal/tail fanning as 0.5 s (from a mean of 30 events) in order to calculate combined counts and durations for dorsal/tail fanning and pectoral fanning together, hereafter *fanning.*

Table 2.1: Ethogram showing the recorded egg-tending behaviours of *Pomacentrus amboinensis* males.

Behaviour	**Description**	**Elements**
Nest visit	When the male was underneath the artificial nest.	Count, duration, duration of intervals between events
Pectoral fanning	When the male faced the brood, fanning with its pectoral fins and often pecking at the clutch with its mouth.	Count, duration
Dorsal/tail fanning	When the male wriggled the length of its body along the eggs, with the dorsal fin in contact with the clutch.	Count, duration approximated
Fanning	Pectoral fanning + dorsal/tail fanning.	Count, duration
Nest maintenance	When the male exhibited tidying of the nest, including removing objects (e.g. shells), mouth-pecking away from the brood, and digging in the substrate.	Count
Vigilance	When the male was stationary in the nest entrance, looking out.	Count, duration

2.3.4 Statistical analysis

I calculated rates (for counts) and time-budget percentages (for durations) by dividing the data by the total time the fish spent inside the nest in that period. The change from the baseline period (ambient-sound conditions) to the treatment period (motorboat-noise exposure or ambient-sound control), hereafter *treatment response,* was calculated for each behavioural measure. I analysed the treatment responses in the two trials as paired data for each fish (n = 34) in R V3.5.2 (R Core Team 2018), using paired t-tests and Wilcoxon signed-ranks tests, depending on whether the data met the assumptions of parametric testing. Where a significant difference in response between treatments was found, one-sided t-tests were used to determine whether there was a significant change from the baseline in each treatment. Three pairs of data were omitted from the analysis of the mean interval between nest visits, due to one of each pair being judged an extreme outlier (values were outside upper or lower quartile ± 8 x interquartile range). Values presented in the Results are means ± standard error of the means (SEM). Significance was assumed where $p < 0.05$.

2.4 Results

2.4.1 Nest visits

Male *P. amboinensis* spent 158.7 ± 14.1 s in the nest in the 10-min baseline period, visiting the nest for 9.1 ± 0.7 s at a time every 30.3 ± 2.6 s. There were no significant differences between the treatment responses in: the total time spent inside the nest, hereafter *nest time* (paired t-test: $t_{33} = 0.48$, $p = 0.633$; Figure 2.2a); the mean duration of nest visits (Wilcoxon test: $V_{33} = 386$, $p = 0.13$; Figure 2.2b); or the mean interval between visits ($V_{30} = 334$, $p = 0.094$; Figure 2.2c).

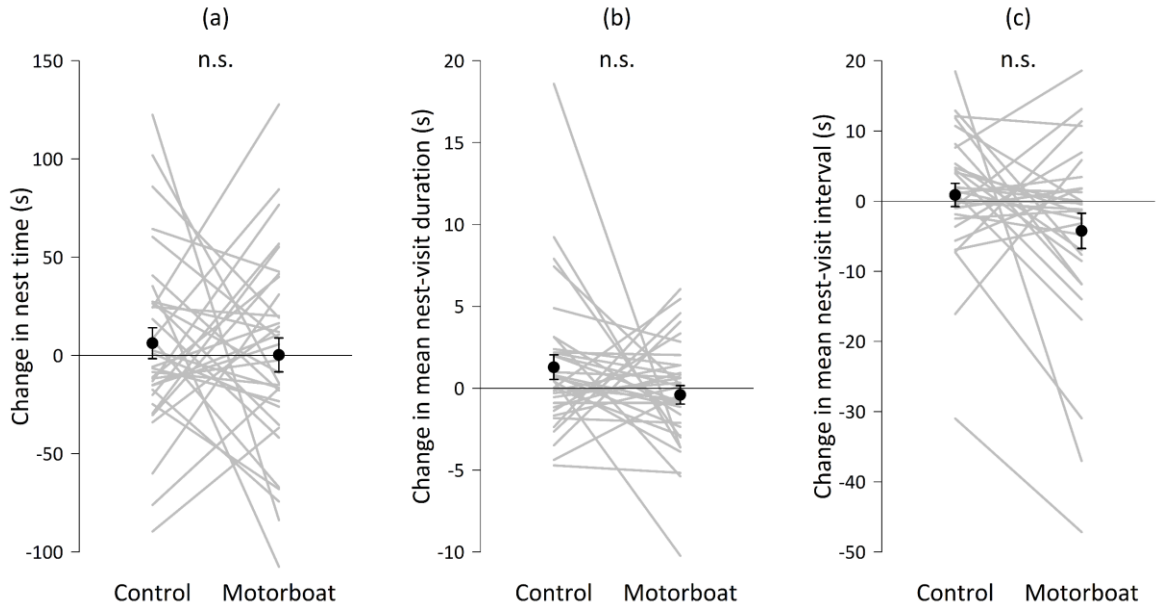

Figure 2.2: Sound-treatment responses in (a) total time in nest (n = 34), (b) mean duration of each nest visit (n = 34) and (c) mean interval between nest visits (n = 31) by male *Pomacentrus amboinensis*. Black points show mean treatment responses ± SEM error bars; grey lines show paired data from individuals. n.s. = not significant.

2.4.2 Egg-tending behaviours

Fanning occurred at a baseline rate of 17.5 ± 1.4 events per min of nest time, for 38.4 ± 1.7% of nest time. There was no significant difference between the treatment responses in fanning rate (Wilcoxon test: $V_{33} = 306$, $p = 0.893$; Figure 2.3a). However, there was a significant effect of treatment on the response in percentage of nest time spent on fanning (paired t-test: $t_{33} = 2.34$, $\mathbf{p = 0.026}$; Figure 2.3b),

which significantly decreased in the motorboat-noise trials (one-sided t-test: t_{33} = -2.27, ***p* = 0.030**) but did not significantly change in the control trials (t_{33} = 1.24, p = 0.222).

Nest maintenance occurred at a baseline rate of 0.4 ± 0.1 events per min of nest time. There was no significant difference between treatment responses in nest-maintenance rate (Wilcoxon test: V_{33} = 175, p = 0.484; Figure 2.3c).

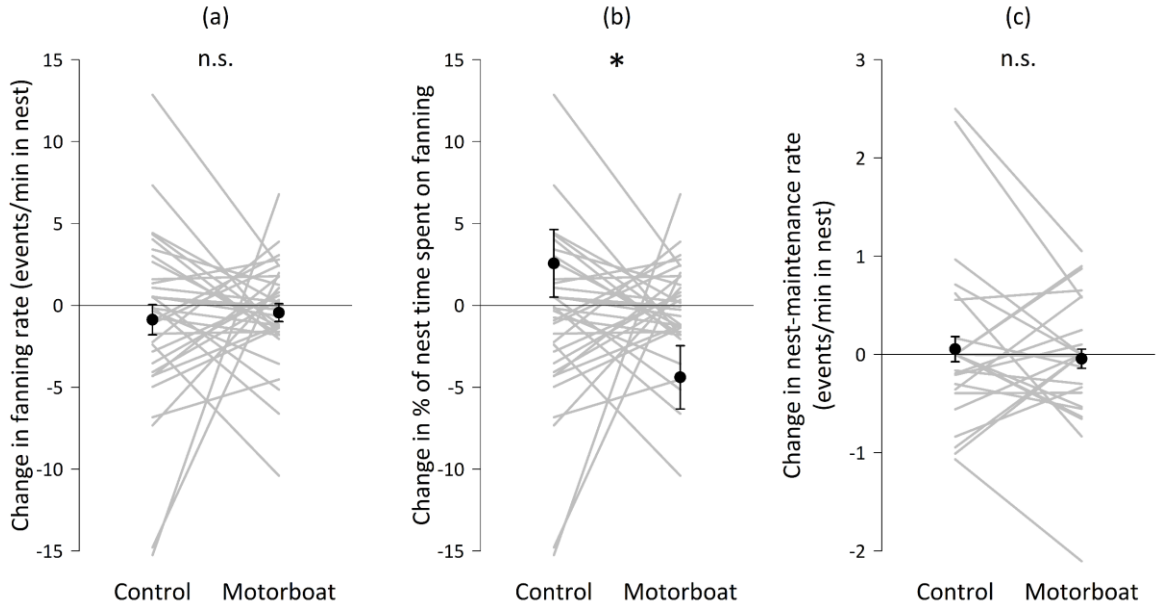

Figure 2.3: Sound-treatment responses in (a) fanning rate, (b) percentage of nest time spent on fanning and (c) nest-maintenance rate by male *Pomacentrus amboinensis* (n = 34 for all response measures). Black points show mean treatment responses ± SEM error bars; grey lines show paired data from individuals. n.s. = not significant, * $p < 0.05$.

2.4.3 Vigilance behaviour

Vigilance occurred at a baseline rate of 3.3 ± 0.3 events per min of nest-time, occupying 8.5 ± 0.7% of nest time. There was a significant effect of treatment on the response in vigilance rate (Wilcoxon test: V_{33} = 116, ***p* = 0.001**; Figure 2.4a), which significantly increased in the motorboat-noise treatment (one-sided t-test: t_{33} = 3.11, ***p* = 0.004**) and did not significantly change from the baseline in the control treatment (t_{33} = -1.86, p = 0.072). There was also a significant effect of treatment on the response in percentage of nest time spent on vigilance (Wilcoxon test: V_{33} = 182, ***p* = 0.048**; Figure 2.4b): a

significant increase in the motorboat-noise treatment (one-sided t-test: t_{33} = 2.24, ***p* = 0.032**) compared to no significant change from the baseline in the control treatment (t_{33} = -0.66, p = 0.516).

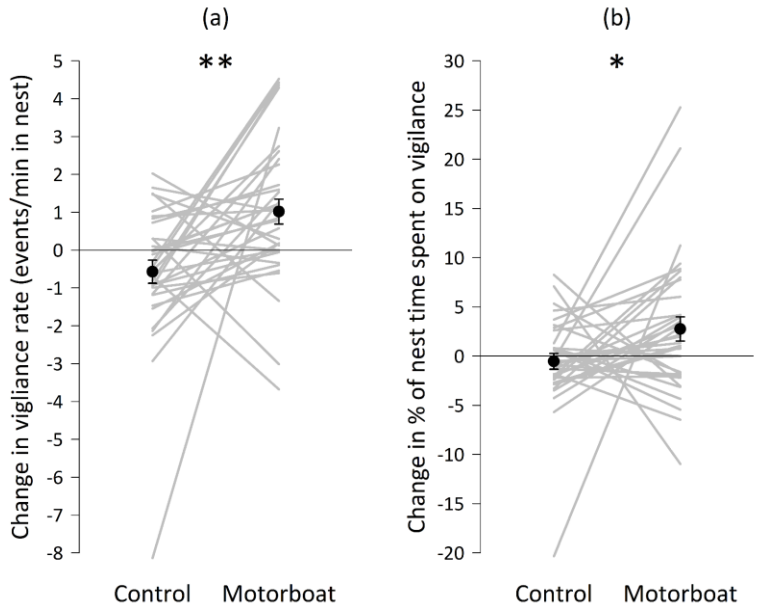

Figure 2.4: Sound-treatment responses in (a) vigilance rate and (b) percentage of nest-time spent on vigilance by male *Pomacentrus amboinensis* (n = 34 for both response measures). Black points show mean treatment response ± SEM error bars; grey lines show paired data from individuals. * $p < 0.05$, ** $p < 0.01$.

2.5 Discussion

These results show that some parental-care behaviours of wild male *P. amboinensis* in natural conditions are detrimentally affected by exposure to noise from real motorboats. Egg-tending males experiencing motorboat noise significantly decreased the percentage of time spent fanning the eggs and increased the percentage of time spent on vigilance compared to control fish. However, males did not significantly change how often nest visits occurred or the duration of nest visits, nor did they change the rate of nest-maintenance behaviours when exposed to motorboat noise compared to ambient-sound conditions.

The decrease in fanning during motorboat-noise exposure could be due to distraction (Chan et al. 2010; Purser and Radford 2011) or physiological stress (Simpson et al. 2015; Celi et al. 2016; Vazzana et al. 2017), causing the male to spend more time on other behaviours or to shelter in the

nest without performing any alternative behaviours. Frequent fanning of the clutch with the pectoral and dorsal fins ventilates the eggs, which increases oxygen consumption and promotes development and survival (Zoran and Ward 1983). Additionally, fanning is often accompanied by mouth-pecking at the clutch to remove damaged, dead or diseased eggs (Blumer 1979); this was likely also reduced in motorboat-noise trials. The noise-induced decrease in fanning and associated mouth-pecking could therefore decrease the hatching success of clutches exposed to motorboats. Embryonic development has been shown to be compromised by noise exposure in the spiny chromis (Fakan and McCormick 2019) and the sea hare *Stylocheilus striatus* (Nedelec et al. 2014), although the hatching success of captive daffodil cichlids was unaffected by noise playback (Bruintjes and Radford 2014). While hatching success was not recorded in the current study, the reduction in fanning suggests egg mortality in noisy environments could be determined by indirect effects on parental care, alongside any direct effects on the embryos. Consequently, repeatedly exposed males could have reduced breeding success if this response persisted. Furthermore, this potential for individual declines in fitness could have an effect at the population level, with decreased juvenile recruitment in noisy environments. Coral-reef larval recruitment can be disrupted by noise due to direct effects on larval soundscape orientation (Holles et al. 2013; Simpson et al. 2016a), so this combination of direct and potential indirect effects could also have a compound impact on populations.

As *P. amboinensis* significantly increased both the rate and percentage of nest time spent on vigilance during the noise exposure, these fish may be investing more in anti-predator tactics at the expense of fanning during noise; a trade-off which has previously been considered in ambient conditions (Lissåker and Kvarnemo 2006), as both fanning and vigilance are energetically costly for the parent (Hinch and Collins 1991). Additionally, vigilance may be used to look for receptive females from the safety of the nest; another known behavioural trade-off with parental care (Magrath and Komdeur 2003). If the fish are using acoustic cues to locate or identify predators, intruders or receptive females, these cues may be masked by the motorboat noise (Vasconcelos et al. 2007; Sebastianutto et al. 2011). Therefore, increasing vigilance may be a compensatory response to decreased reliability of acoustic cues, with the fish investing more in collecting visual information instead (McCormick et al. 2018). Vigilance can improve response times to threats such as egg-predators or competitors, with consequences for individual as well as clutch survival (Krause and Godin 1996). The increase in vigilance found here could be due to fish attempting to identify the source of the noise visually or perception of the noise as a threat (Spiga et al. 2017), a behavioural trade-off which in this case would have no benefit to the individual as no real threat is present. Alternatively, if the motorboat-noise exposure also affected the community composition around the nest, the fish could be responding to genuine increased predation risk; increased vigilance would then be an appropriate response and may

improve survival rates in noisy environments. However, previous work has shown that juvenile *P. amboinensis* become more stressed and less effective at avoiding model predators, and suffer more predation from real predators, during both playback and real motorboat noise (Simpson et al. 2016b). This implies that the anti-predator behaviours of *P. amboinensis* are compromised by noise, which suggests that the vigilance response in the current study is not an improved anti-predator response but may instead be a result of distraction (Chan et al. 2010; Purser and Radford 2011) or a compensatory modality shift from gathering acoustic cues to gathering visual cues.

Males in the study did not significantly alter their typical nest-visiting routine when exposed to noise; the fish did not leave the nest unattended for longer intervals or abandon the nest. This is unsurprising due to the high value of the nest site (Picciulin et al. 2010), as there is a high likelihood of losing the site to conspecifics if it is left unattended for prolonged periods of time (Hourigan 1986), leading to a loss of both the current clutch and potential future reproductive opportunity. The males also maintained normal levels of sheltering in the nest. A decrease in sheltering could put the fish at more risk from predators, whereas an increase could be detrimental to body condition, with less time available for foraging (McLaughlin and Kunc 2015), thus this lack of response to noise is appropriate and beneficial. The relative investment in behaviours performed when the male is away from the nest, such as feeding and territorial defence, could be impacted by noise (Sebastianutto et al. 2011; Bracciali et al. 2012), however the current experiment considered events within the nest only.

The rate of nest maintenance was not significantly affected by motorboat-noise exposure in this study. Maintenance includes removing objects (e.g. shells), mouth-pecking to remove algae from the egg-laying surface and digging in the substrate (Moyer 1975). These behaviours could affect female choice (Hastings 1988; Sikkel 1995), as a well-maintained nest could signal a high-quality male, provide an appropriate spawning surface and may reduce the occurrence of disease (Constantz 1985). It may be inferred from the lack of effect on nest-maintenance behaviours that these aspects of female choice and effects of cleanliness are unaffected by motorboat noise.

This experiment only considered the effects of a single, short-term exposure to motorboat noise. Previous work has shown that fish have the potential to recover rapidly from the effects of noise after exposure ends (Bruintjes et al. 2016; Holmes et al. 2017), and reduce responses following repeated or long-term exposure through habituation or desensitisation (Nedelec et al. 2016b; Radford et al. 2016). Individual recovery from short-term noise could allow breeding success to remain at normal levels, despite the initial perturbation to parental-care behaviours during noise. Given the increasing abundance and distribution of sources of marine noise pollution, it is likely that more organisms will become exposed to noise repetitively and chronically throughout their life cycles. It is

therefore essential that additional evidence is collected regarding long-term effects of these types of exposures, which will aid the development of mitigation policy addressing realistic temporal patterns of exposure.

Since the breeding habits of *P. amboinensis* are representative of other pomacentrids, although hearing thresholds and vulnerability to stress may vary between species (Barton 2002; Wright et al. 2010), the effects found in this study could be widespread among fish communities. For this study, reproductive output was not measured; however, I predict that population-level reproductive success of other pomacentrids could decline as anthropogenic noise pollution increases, at least in part due to effects on parental-care behaviours during key developmental stages. Future studies on the effects of boat noise on parental care would benefit from measuring reproductive output and quantifying population-level effects to explore this prediction further.

There is already enough knowledge on the negative effects of motorboat noise to begin designing and testing mitigation strategies for this pollutant. Researchers should integrate mitigation strategies into experiments when testing new hypotheses on noise effects, and policymakers and individuals should begin to implement simple strategies to moderate boat noise. For example, some studies have already shown the reduced impact on fish of 4-stroke boat engines versus noisier 2-stroke versions (Jain-Schlaepfer et al. 2018; McCormick et al. 2018). Mitigation strategies could also be targeted at specific negative impacts: from this study, an emerging recommendation would be to exclude vessels from habitats specifically during the breeding season of key organisms to prevent changes in parental-care behaviours. The ecological functions and services these habitats provide give policymakers high incentive to protect coral-reef species, and there is the potential to manage motorboat noise with low cost – high gain solutions.

CHAPTER THREE

Limited effects of short-term and long-term motorboat noise on territorial defence in a brooding coral-reef fish, *Acanthochromis polyacanthus.*

Chapter contributions:

Experimental design –

Sophie L. Nedelec, Andrew N. Radford, Stephen D. Simpson.

Fieldwork –

SLN (lead), Kasey Barnes, Isla K. Davidson, Tim A. C. Gordon, Mark I. McCormick, Kieran P. McCloskey, Brendan Nedelec, Olivia Rose, SDS, Maggie Travers, Sam Wines.

Video and statistical analysis and write-up –

Katherine E. Chapman.

3.1 Abstract

Marine environments are subject to increasing levels of noise pollution from human activity. A range of physiological and behavioural impacts on organisms has been demonstrated, yet evidence of the effects of long-term exposures on fitness-affecting behaviours is limited. A month-long field experiment was used to investigate the impacts of anthropogenic noise on larval defence, a key parental-care behaviour, in a wild population of an abundant coral-reef fish *Acanthochromis polyacanthus.* Parents were either subjected to daily exposure to a common source of noise pollution, motorboats, or allowed to remain in natural ambient-sound conditions (as a control). Long-term exposure to motorboat noise had no significant effect on the baseline defensive behaviours of these fish. Although displays to territory intruders initially decreased in response to short-term noise, this effect did not persist after the short-term exposure ceased. Increases in this behaviour in response to short-term noise were found after a week of repeated exposure, with sensitisation to short-term noise as the long-term exposure regime continued. Significant noise-related effects on the striking behaviour of parents were only found for attacks on non-piscivores, where sensitisation over the month in the response to short-term noise also occurred. This study emphasises the need for more experimental investigation in natural conditions of the effects of long-term exposures to real noise sources on behaviours with a close relationship to fitness.

3.2 Introduction

Anthropogenic noise is prevalent in marine environments due to extensive human activities, including military actions, construction, natural-resource exploitation and, significantly, vessel traffic (review: Hildebrand 2009). Noise pollution from traffic, including fishing, recreational boating and shipping, is growing in intensity, particularly around coastal areas (Pine et al. 2016), where important habitats such as coral reefs are located. Many studies have already shown the detrimental effects of boat noise on the physiology and behaviour of organisms across a range of taxa (reviews: Gill et al. 2015; Kunc et al. 2016; Shannon et al. 2016). Most importantly, there is some evidence that vessel noise could negatively impact fitness-affecting factors by, for instance, disrupting development (Nedelec et al. 2014), reducing in anti-predator responses (Simpson et al. 2015) or decreasing breeding success (de Jong et al. 2018).

A large number of studies have demonstrated various effects of oceanic noise pollution on fish. Physiological changes have been shown in multiple species exposed to noise, such as increased haematological stress indicators and ventilation rates, which are taken as proxies of stress (Simpson et al. 2005; Crovo et al. 2015; Vazzana et al. 2017). Motorboat-noise playback has also been shown to affect embryonic development negatively in the spiny chromis *Acanthochromis polyacanthus* (Fakan and McCormick 2019). Behavioural changes documented include reduced prey intake in noisy conditions by the European minnow *Phoxinus phoxinus* (Voellmy et al. 2014a), and increased sheltering during motorboat-noise playback in the red-mouthed goby *Gobius cruentatus* (Picciulin et al. 2010). Noise can also have masking effects, with the potential for boat noise to disrupt acoustic communication between conspecifics in Mediterranean chromis *Chromis chromis,* brown meagres *Sciaena umbra* and red-mouthed gobies (Codarin et al. 2009). This selection of examples emphasises the variety of negative effects anthropogenic noise can have on fish, any of which could lead to decreased fitness.

Parental-care behaviours in fish are poorly represented in the anthropogenic-noise literature but deserve more attention owing to the direct link to offspring survival. Furthermore, these behaviours are widespread: 89 families of teleosts have species which exhibit parental care (Blumer 1982), with behaviours including nest maintenance (Hale and St Mary 2007), egg tending (Zoran and Ward 1983), provisioning (Buckley et al. 2011) and defence against competitors and predators (Haley and Müller 2002). Previous studies have shown that noise playback can be detrimental to nest maintenance – for example, lower rates of nest digging in captive male daffodil cichlids *Neolamprologus pulcher* (Bruintjes and Radford 2013) – and to egg tending, with a reduction found in Mediterranean chromis (Picciulin et al. 2010) and Ambon damselfish *Pomacentrus amboinensis*

(Chapter 2). Although some studies have shown negative effects of noise on territoriality (Sebastianutto et al. 2011), this has rarely been studied in the context of guarding offspring. Nedelec et al. (2017a) conducted a 12-day noise-exposure experiment on larval-guarding pairs of free-swimming spiny chromis, and found an increase in nest-defence behaviours by the parents but higher offspring mortality at nests experiencing motorboat-noise playback compared to ambient-sound playback controls. The authors suggest that noise-induced stress may be causing higher levels of aggression but that the parents could be less effective in their defence, hence the increase in offspring mortality.

Although there is a growing body of evidence on the effects of anthropogenic noise on fish behaviour, these studies have mostly used tank-based experiments and/or playback of noise, and have tended to focus on short-term exposures. Only a few studies have collected data in natural habitats and/or used real noise sources in experiments. For example, exposure to real motorboats caused an increased heart rate in embryonic staghorn damselfish *Amblyglyphidodon curacao* (Jain-Schlaepfer et al. 2018) and a reduction in anti-predator responses in the Ward's damselfish *Pomacentrus wardi* (McCormick et al. 2018). Simpson et al. (2016b) found that motorboat-noise exposure, both in laboratory playbacks and with real motorboats in field conditions, caused an increase in oxygen consumption, disrupted an anti-predator escape response, and increased mortality by predation in the Ambon damselfish. There are also only a few experiments that have addressed recovery from noise exposure, and the effects of repeated and long-term exposures. Recovery of normal ventilation rates after initial increases were found in both the domino damsel *Dascyllus trimaculatus* over two weeks of noise exposure (Nedelec et al. 2016b) and the European seabass *Dicentrarchus labrax* over 12 weeks of exposure (Radford et al. 2016). Repeated exposure to real boat noise caused brown meagres to alter their courtship vocalisations as compensation for masking effects (Picciulin et al. 2012). Behavioural responses to noise have also been shown to attenuate over repeated exposures in European seabass (Neo et al. 2018).

The aim of the current study was to advance the understanding of the impacts of anthropogenic noise by experimentally testing the effects of long-term noise exposure on fitness-affecting behaviours in a wild population of free-swimming fish, using a real, ecologically relevant noise source (motorboats). The study species *Acanthochromis polyacanthus* (family Pomacentridae) is a common Indo-Pacific damselfish. Whereas most coral-reef fish larvae undertake a pelagic phase to avoid the high predation pressures of the reef, *A. polyacanthus* is one of only three damselfish species (Bernardi 2011) to exhibit biparental care of juveniles within the adult territories throughout the larval stage, which lasts for weeks or months (Kavanagh 2000). The parents aggressively defend nesting territories from potential predators and other intruders throughout the breeding season

(Robertson 1973), using warning displays, chasing and biting; larvae depend on these parental behaviours for survival (Nakazono 1993). Defensive behaviours additionally provide benefits to the parents by expelling conspecific competitors for space and food. This species was chosen for its abundance at the study site, high site-fidelity, territoriality and the long duration of the parental-care period.

The territorial behaviours of larvae-guarding pairs of *A. polyacanthus* were recorded at natural nests under either a month-long motorboat-noise exposure regime or an equivalent period of natural ambient sound (as a control). I aimed to determine whether short-term and long-term noise exposure affect this aspect of parental care: (1) to infer whether impacts of motorboat noise on parental behaviours could provide an explanation for the reduced larval survival found by Nedelec et al. (2017a); and (2) to investigate the potential for recovery from short-term and long-term motorboat-noise impacts in this species. I hypothesised that these behaviours would be negatively influenced by noise in the short term, through a reduction in either the frequency or appropriateness of defence, for example if the parents attacked predators less often in favour of attacking non-piscivores. Furthermore, I predicted that the fish would experience behavioural carry-over effects after the end of the exposure, but that the effects of noise would attenuate following repeated exposures.

3.3 Methods

3.3.1 Field methods

Videos of free-swimming breeding pairs of *Acanthochromis polyacanthus* guarding broods of larvae were collected by colleagues from October 2017 to January 2018 at Lizard Island Research Station, Queensland, Australia (14°4′S 145°28′E). Video recordings were made around natural nests (n = 35) at six sites in the Lagoon area, a shallow (~0.5–10 m deep), sheltered coral-reef flat. Three of the sites were allocated a long-term motorboat-noise treatment (n = 19 nests) and three were allocated an ambient-sound treatment as a control (n = 16 nests). Motorboat-noise treatment sites were experimentally exposed five times a day throughout the season to engine noise from a 5-m long motorboat (30 hp 4-stroke outboard motor) driven continuously for 15 min in the vicinity of the site in a figure-of-eight route approximately 10–100 m away from the reef edge. Eight different motorboats were used throughout the season to minimise pseudoreplication. Control sites only experienced motorboat noise when researchers approached and departed the site on recording days, or from occasional unregulated boats external to the experiment, which were also present at the motorboat-noise sites. As part of a larger study, *A. polyacanthus* behaviour was recorded on video

approximately every 4 days at each nest, from the hatching date until larvae were no longer present or until the end of the field season. One static, mounted GoPro Hero 5 camera was used per nest, positioned by a snorkeler who immediately left the area. Fish were allowed 5 min to resume normal behaviour following this disturbance (Nedelec et al. 2016b). Each trial began with a 5-min recording period in ambient-sound conditions to determine baseline pre-exposure behaviours. This was followed by one of the daily 15-min exposures in the motorboat-noise treatment, or a 15-min ambient-sound exposure in the control treatment. A 5-min post-exposure period in ambient-sound conditions was also recorded for both treatments.

3.3.2 Acoustic characterisations

The experiments in Chapter 2 and Chapter 3 were undertaken with the same motorboats at the same location, with overlapping sites. The acoustic characterisations of the sound treatments are detailed in Chapter 2 (2.3.2 Acoustic characterisations).

3.3.3 Behavioural data extraction

The fieldwork season yielded over 200 videos, each showing one trial on one day at a nest (n = 35 nests). For parents which produced more than one brood during the field season (n = 6 nests), I only considered the first brood of the season. The majority of nests were active with a first brood within the first month of the long-term experiment. Additionally, the mean survival age of broods was 21 days (n = 44 nests, including nests not video-recorded for this study). For these reasons, I selected trials with larval ages 1–4 days and 8–11 days and with fewer than 30 days exposure (n = 33 nests) for analysis. Nests were rarely filmed more than once within a time window; in these cases (n = 3), I selected the recording from the earlier day. This resulted in a total of 18 nests from the motorboat-noise treatment and 15 nests from the ambient-sound treatment, with one or two trials from each nest (n = 57 trials).

I cropped the videos using ffmpeg (open source: ffmpeg.org) to produce four 5-min periods per trial: (1) pre-exposure (baseline), (2) first 5 min of exposure, (3) last 5 min of exposure and (4) 5 min post-exposure. These periods were chosen to investigate: (1) the effects of long-term repeated motorboat-noise exposure on baseline behaviours; (2) the initial responses to the onset of short-term motorboat noise; (3) any changes in responses to prolonged short-term motorboat noise; and (4) whether behaviours returned to baseline levels or whether carry-over effects occurred immediately after the motorboat-noise input ended. The start times of the different periods were calculated from

a combination of audio and visual cues. The cropped videos were saved with coded file names and were watched with no sound so that I was blind to the treatment and period.

I collected behavioural data on the two *A. polyacanthus* parents (Table 3.1) using the behavioural observation software BORIS (Friard and Gamba 2016). I recorded strikes and displays separately for each parent, so that simultaneous behaviours aimed at the same recipient were recorded as separate events. In videos with more than two *A. polyacanthus* individuals, I identified focal parents through their proximity to the nest and the larvae, and by exhibited defensive behaviours, as well as lack of interaction with one another. To the best of my knowledge, no attacks occurred between co-parents.

Table 3.1: Ethogram showing the recorded territorial behaviours of larvae-guarding *Acanthochromis polyacanthus* at natural nests.

Behaviour	**Description**	**Elements**
Absence	When parents were off-screen or obscured (e.g. by habitat features) so that behaviours could not be observed.	Duration
Display	When a focal fish raised its dorsal fin vertically, sometimes accompanied by tilting the body with the nose pointed downwards.	Count
Strike	When a focal fish swam rapidly at an intruder, chasing it from the territory; sometimes accompanied by biting.	Count – categorised by recipient (conspecific, heterospecific piscivore, heterospecific non-piscivore)

Additionally, I estimated the counts of three categories of non-focal fishes over 30 s in the middle of each 5-min period: non-focal conspecifics, heterospecific piscivores and heterospecific non-piscivores were counted, including all identifiable fishes on screen. This estimate was taken to determine whether any changes in the parental behaviours could be due to the noise exposure affecting the abundance of other fishes around the nest. Fishes that were not identifiable to family (e.g. due to distance) were not included, and all fishes coming on-screen were assumed to be new individuals. I identified piscivorous families using the Lizard Island Field Guide (Hoggett 2019) and

FishBase (Froese and Pauly 2000), and assumed all species within these families to be potential larval predators (Table A.1, Appendix). No other predators (e.g. Octopoda) were observed.

3.3.4 Statistical analysis

I calculated how long parental behaviours were observable (i.e. for how long parents were on-screen) for each 5-min period. Observation time (s) = 2 x time both parents were on screen + time only one parent was on screen. I used these values (1) as an offset variable in the pre-exposure behavioural-count models, and (2) to calculate rates for each recorded behaviour for all other analyses. Two videos with observation times shorter than 60 s were discarded to avoid artificial inflation of behavioural rates (resulting in n = 55 trials).

All analyses were completed in RStudio V1.1.463 (R Core Team 2018) using linear mixed-effect models (LMMs) and generalised linear mixed-effect models (GLMMs) in the *lme4* package (Bates et al. 2015). All models had long-term treatment (motorboat noise, ambient sound control) as a fixed effect and nest identity nested within site identity as random effects to account for non-independence. The models were first run with larval age as a continuous fixed effect to determine if there was an age effect (Table A.2, Appendix). Subsequently, in cases where age was not found to have a significant effect, models included days since the start of the long-term exposure regime as a fixed effect instead of age (Table A.3, Appendix). If a significant effect of age was found, data from the two age windows (1–4 days, 8–11 days) were analysed with separate models due to the correlation between larval age and days of exposure (Pearson correlation coefficient = 0.56). The assumptions of parametric testing were checked for each model, and LMMs or GLMMs were selected accordingly.

To investigate the effect of long-term motorboat-noise exposure, but without current exposure, I analysed the behavioural rate and community counts from the pre-exposure periods (n = 55 trials), using GLMMs (negative binomial; link = log). Additionally, I analysed the proportions of strikes to each category of recipient using GLMMs (binomial; link = logit): for conspecifics vs heterospecifics, I analysed the subset of data when strikes occurred to identified recipients (n = 40 trials); and for heterospecific piscivores vs heterospecific non-piscivores, I analysed the subset of data when strikes occurred to identified heterospecifics (n = 39 trials).

To investigate any immediate effect of short-term motorboat-noise exposure, I calculated the changes in behavioural rates and community counts from the pre-exposure period to the first 5 min of exposure (n = 55 trials). I analysed the changes in rates and counts using LMMs (Gaussian). One trial was omitted from the analyses of total strike rate and strike rate to conspecifics (n = 54 trials), as it

was deemed an extreme outlier in these measures (outside lower quartile - 7 x interquartile range) with a disproportionate effect on the model fits. Similar analyses were used to determine whether behavioural changes occurred between the first and last 5-min periods of exposure (n = 53 trials), and between the pre-exposure and post-exposure periods (n = 43 trials); lower sample sizes in these analyses were due to the absence of the last 5-min period of exposure or the post-exposure period.

Data presented in the Results are means ± standard errors of the means. Significance was assumed where $p < 0.05$.

3.4 Results

3.4.1 Long-term noise-exposure regime (baseline, pre-short-term exposure) (Table A.3a)

Acanthochromis polyacanthus parents displayed at a baseline rate of 0.3 ± 0.1 displays per min and conducted strikes at a baseline rate of 0.7 ± 0.1 strikes per min. Treatment had no significant effect, throughout the long-term exposure regime, on either baseline display rate (GLMM, treatment: z_{48} = -0.11, p = 0.915; days of exposure: z_{48} = 0.29, p = 0.774; interaction: z_{48} = -0.15, p = 0.881) or baseline strike rate (treatment: z_{48} = -1, p = 0.317; days of exposure: z_{48} = 0.85, p = 0.397; interaction: z_{48} = -0.04, p = 0.866). Treatment had no significant effect, throughout the long-term exposure regime, on the proportion of strikes with a known recipient targeted at conspecifics vs heterospecifics (treatment z_{34} = -0.9, p = 0.369; days of exposure: z_{34} = -1.63, p = 0.103; interaction: z_{34} = 1.77, p = 0.077). Similarly, there was no significant effect of treatment, when considering strikes targeted at heterospecifics, on the proportion of strike rates targeted at piscivores vs non-piscivores (treatment z_{33} = 0.35, p = 0.725; days of exposure: z_{33} = 0.72, p = 0.472; interaction: z_{33} = -0.08, p = 0.936).

The estimated abundance of conspecifics around nests was significantly lower at motorboat-noise sites (0.7 ± 0.3) than at ambient-sound sites (3.4 ± 0.7; GLMM: z_{48} = -2.18, ***p* = 0.028**); days of long-term exposure had no significant effect on conspecific abundance (z_{48} = 0.96, p = 0.336) nor did its interaction with the sound treatment (z_{48} = 0.074, p = 0.941). No such significant effect of sound treatment was found for heterospecific piscivores (treatment: z_{48} = -0.16, p = 0.117; days of exposure: z_{48} = -0.26, p = 0.797; interaction: z_{48} = 1.2, p = 0.23) or heterospecific non-piscivores (treatment: z_{48} = -0.03, p = 0.976; days of exposure: z_{48} = 0.99, p = 0.323; interaction: z_{48} = -0.34, p = 0.734).

3.4.2 Introduction of short-term noise exposure (Table A.3b)

The change in display rate when the short-term-exposure period began was significantly affected by the interaction between treatment and days of long-term exposure (LMM: $\chi^2_1 = 4.96$, $\mathbf{p = 0.026}$; Figure 3.1a). In the motorboat-noise treatment, fish increased their display rate at the onset of short-term noise to a greater extent as the long-term exposure regime progressed. In the control treatment, at the start of the month, the fish slightly increased their display rate at the onset of the short-term treatment period, but this response tended towards no change as the month continued.

There was no significant effect of treatment (LMM: $\chi^2_1 = 0.05$, $p = 0.831$), days of long-term exposure ($\chi^2_1 = 0.26$, $p = 0.610$) or their interaction ($\chi^2_1 = 0.437$, $p = 0.509$) on the change in total strike rate when the short-term-exposure period began. Treatment also had no significant effect on the change in strike rate towards conspecifics (treatment: $\chi^2_1 = 1.57$, $p = 0.211$; days of exposure: $\chi^2_1 = 0.16$, $p = 0.689$; interaction: $\chi^2_1 = 0.01$, $p = 0.930$) or heterospecific piscivores (treatment: $\chi^2_1 = 0.11$, $p = 0.744$; days of exposure: $\chi^2_1 = 0.09$, $p = 0.761$; interaction: $\chi^2_1 = 0.104$, $p = 0.747$). There was a significant interaction between treatment and days of long-term exposure affecting the change in parental strike rate against non-piscivores. However, this only occurred within the first larval-age window ($\chi^2_1 = 12.48$, $\mathbf{p < 0.001}$; Figure 3.1b); this interaction effect was not significant in the second larval-age window ($\chi^2_1 = 0.74$, $p = 0.390$; Figure 3.1b). For the first larval-age group, early in the long-term exposure regime, the adults did not change their strike rate towards non-piscivores in response to short-term motorboat-noise exposure, but later in the long-term exposure regime, strike rate against non-piscivores increased at the onset of short-term noise. In the control treatment, early in the month, adult fish increased their strike rate towards non-piscivores at the onset of the short-term treatment period, but later in the month, this rate decreased at the onset of the short-term treatment.

Treatment had no significant effect on the change in abundance estimates of non-focal fish around the nests in response to the short-term treatments, throughout the long-term exposure regime: conspecifics (LMM, treatment: $\chi^2_1 = 2.67$, $p = 0.102$; days of exposure: $\chi^2_1 = 2.30$, $p = 0.129$; interaction: $\chi^2_1 = 0.002$, $p = 0.968$); heterospecific piscivores (treatment: $\chi^2_1 = 0.01$, $p = 0.971$; days of exposure: $\chi^2_1 = 0.17$, $p = 0.681$; interaction: $\chi^2_1 = 0.001$, $p = 0.975$); heterospecific non-piscivores (age 1–4 days, treatment: $\chi^2_1 = 1.18$, $p = 0.277$; days of exposure: $\chi^2_1 = 1.18$, $p = 0.276$; interaction: $\chi^2_1 = 0.47$, $p = 0.493$; age 8–11 days, treatment: $\chi^2_1 = 2.43$, $p = 0.119$; days of exposure: $\chi^2_1 = 1.92$, $p = 0.166$; interaction: $\chi^2_1 = 0.42$, $p = 0.516$).

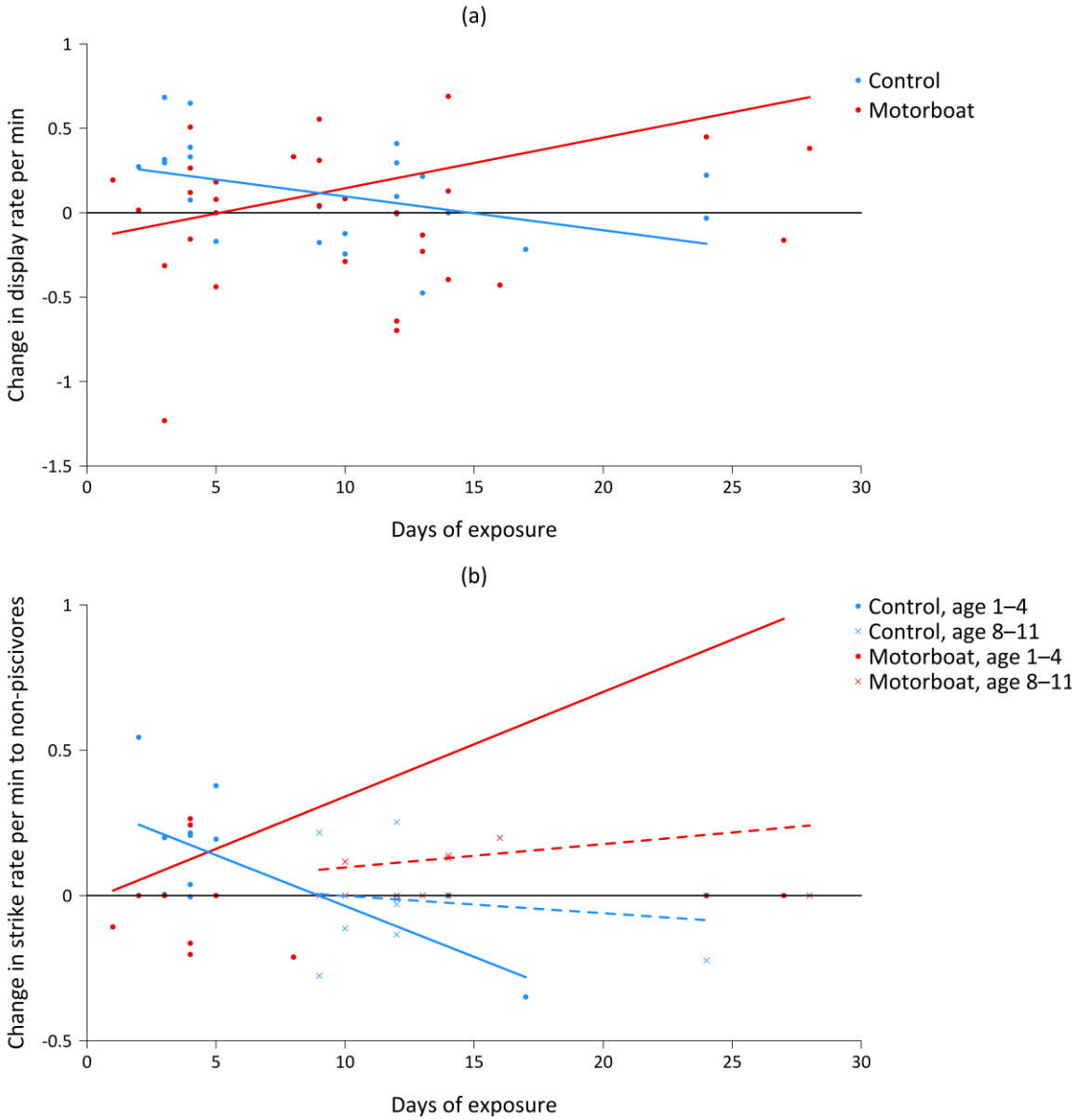

Figure 3.1: (a) The change in display rate by *Acanthochromis polyacanthus* parents from the baseline period to the first 5 min of the short-term exposure period, over the course of the long-term exposure regime. Points show raw data; lines show linear mixed model fits for the two treatments: red = motorboat-noise treatment (n = 30); blue = control (ambient-sound) treatment (n = 25).

(b) The change in strike rate to heterospecific non-piscivores by *A. polyacanthus* parents from the baseline period to the first 5 min of the short-term exposure period, over the course of the long-term exposure regime. Points show raw data and lines show linear mixed model fits: red dots/solid line = motorboat-noise treatment for larval ages 1–4 days (n = 15); blue dots/solid line = control treatment for larval ages 1–4 days (n = 12); red crosses/dashed line = motorboat-noise treatment for larval ages 8–11 days (n = 15); blue crosses/dashed line = control treatment for larval ages 8–11 days (n = 13).

3.4.3 Continuation of short-term noise exposure (Table A.3c)

The change in display rate from the first 5-min period to the last 5-min period of the short-term exposure was not significantly affected by the treatment, throughout the long-term exposure regime (LMM, treatment: $\chi^2_1 = 1.45$, $p = 0.228$; days of exposure: $\chi^2_1 = 0.82$, $p = 0.364$; interaction: $\chi^2_1 = 0.02$, $p = 0.884$). Similarly, the change in strike rate towards intruders between these two sections of the short-term exposure period was not significantly affected by any factor (treatment: $\chi^2_1 = 0.16$, $p = 0.687$, days of exposure: $\chi^2_1 = 0.02$, $p = 0.901$, interaction: $\chi^2_1 = 1.72$, $p = 0.189$).

3.4.4 Post-short-term noise exposure (Table A.3d)

The change in display rate from the baseline period to the post-short-term-exposure period was not significantly affected by treatment, throughout the long-term exposure regime (LMM, treatment: $\chi^2_1 = 0.62$, $p = 0.430$; days of exposure: $\chi^2_1 = 0.001$, $p = 0.973$; interaction: $\chi^2_1 = 0.58$, $p = 0.447$). Similarly, the change in strike rate towards intruders between these two periods was not significantly affected by treatment ($\chi^2_1 = 0.30$, $p = 0.584$), and although days of exposure did have a significant effect on the change in strike rate ($\chi^2_1 = 8.01$, $\mathbf{p = 0.005}$), this did not significantly interact with the sound treatment ($\chi^2_1 = 0.07$, $p = 0.787$).

3.5 Discussion

Motorboat-noise exposure had a limited impact on the defensive parental-care behaviours of *Acanthochromis polyacanthus* guarding larvae. The baseline display and strike rates by parents were unaffected by long-term repeated exposure to motorboat noise. Short-term exposure initially caused a minor decrease in territorial warning displays, however the display rate increased at the onset of short-term noise as the long-term exposure regime continued. Contrary to expectation, fish recovered the baseline displaying rate immediately after the short-term noise stopped, having maintained the heightened response level throughout the 15-min short-term exposure. Surprisingly, motorboat-noise exposure only significantly affected striking directed at non-piscivores during short-term noise exposure, having no effect on overall strike rate or strikes to conspecifics or heterospecific piscivores.

The baseline defensive parental-care behaviours of *A. polyacanthus* were unaffected by daily repetition of motorboat-noise exposure over the course of a month. To the best of my knowledge, this is the longest experimental exposure regime tested on a wild population of fish. The lack of long-term impact on parental care found in the current study is positive for the fish, as reduction in the

efficiency of defensive behaviours could lead to increased larval predation in single broods. Such reproductive impacts could subsequently have population-level effects, such as lower recruitment of juveniles at noise-polluted sites. Surprisingly, repeated noise exposure might be beneficial to *A. polyacanthus* parents, as there were fewer conspecifics present around noise-exposed nests compared to ambient-sound sites, therefore less competition for the nest-site, and potentially lower predation risk. However, given that there were no significant changes in the types of intruders targeted by strikes in the baseline period, the lower conspecific abundance probably did not influence defensive behaviours in these parents.

Territorial displays are a low-cost warning signal directed at potential intruders, including predators and conspecifics, and are assumed to be less energy intensive and less risky than strikes (Haley and Müller 2002). The change in display rate in response to short-term motorboat noise may have been due to the fish experiencing stress (Simpson et al. 2016b; Jain-Schlaepfer et al. 2018), however the fish did not escalate their defensive behaviour towards predators; perhaps striking is reserved for high-threat intrusions only (Haley and Müller 2002), even in stressed fish. Alternatively, the noise may have been perceived as a threat itself (Picciulin et al. 2010; McCormick et al. 2018), but the parents could not locate the source to attack it directly with a strike. It is also possible that displays may be more successful at deterring intruders – which may be stressed themselves – during noise exposure and therefore escalation to a strike was not required; however, there was no complementary decrease in strikes found here. If vocalisations are used as predator deterrents in ambient conditions (Sebastianutto et al. 2011), the increase in displays could be to compensate for masking effects experienced during noise exposure. Displaying without striking may be the sub-optimal response to territory intrusion, but the fish might not have had enough energetic reserves to respond effectively to this increased perception in threat due to reduced feeding or increased metabolic stress during noise exposure (Bracciali et al. 2012; Simpson et al. 2016b). The changes in display rate were not driven by changes in community composition, assumed to indicate threat level, as no change was found in the numbers of heterospecific piscivores or conspecifics – which can also consume larvae – following the onset of short-term noise.

The significant changes in the strike rate against heterospecific non-piscivores in the first larval-age window could be explained by parents making more mistakes when the larvae are younger, given that this result was not found in the older age group. Increasing strikes to non-piscivores is a seemingly ineffective response to noise in terms of larval defence, since non-piscivores should present no threat to the larvae, although non-piscivores could be competing with the parents for food or territorial space (Ceccarelli et al. 2005). The presence of the motorboat noise may have caused stress or distraction so that more of these inappropriate attacks were made, as predicted, with a heightened

effect when the larvae were smaller and perhaps more vulnerable. However, although parental energetic expenditure may have been affected, it is unlikely that this had much effect on the survival of the offspring, as this response did not cause a complementary decrease in defence against conspecifics or heterospecific non-piscivores.

The increases in both the display rate and the strike rate to non-piscivores during short-term motorboat-noise exposure increased in magnitude as the long-term repeated exposure continued, which could indicate sensitisation to motorboat noise. By contrast, in other fish studies there has been evidence of declining responses following repeated noise exposure, including in ventilation rates (Nedelec et al. 2016b; Radford et al. 2016) and swimming patterns (Neo et al. 2018). The greater increase in displays and strikes to non-piscivores following repeated noise-exposure in the current study may be a result of cumulative stress or a growing perception of threat. The lack of change in piscivore and non-piscivore abundance around nests over the long-term exposure indicates that sensitisation, rather than changing risk, is the most likely cause of the long-term increases in response.

The display rate and the strike rate to non-piscivores returned to baseline levels after the end of the short-term noise exposure. Rapid recovery from noise-induced stress was also found in the ventilation rate of European seabass and European eels *Anguilla anguilla* (Bruintjes et al. 2016), and behavioural recovery has been demonstrated in the Ambon damselfish following motorboat-noise exposure (Holmes et al. 2017). The detrimental effects of chronic stress are well documented for fish and include reduced growth rate (Gregory and Wood 1999), reduced nutritional intake (Santos et al. 2010) and altered reproduction (review: Schreck, Olla and Davis, 1997). The rapid return to baseline behaviours found in the current study was therefore likely to be beneficial to the *Acanthochromis polyacanthus* parents, as this suggests there were no carry-over effects of stress beyond the noise-exposure period, although no proxies of physiological stress were measured here. Alternatively, it suggests that distraction or masking of acoustic communication between the parents occurred during the noise exposure (Codarin et al. 2009; McCormick et al. 2018), so that once the noise ceased there was no longer interference and the fish could resume normal behaviour. The rapid recovery of normal parental care by this fish is a positive outcome in face of ever-increasing boat-noise intensities around vulnerable coral-reef ecosystems.

One of the aims of this experiment was to determine whether changes in parental-care behaviours could explain the higher mortality during motorboat-noise playback of *A. polyacanthus* larvae found by Nedelec et al. (2017a). They found a higher rate of striking behaviours by male parents exposed to noise compared to an ambient-sound control. This was partially repeatable in defensive displaying, after multiple short-term exposures, but not in the overall striking behaviour of parents in

this experiment. Differences in the results between these experiments could have resulted from several differences between the studies. Nedelec et al. only considered the behaviours of the male, rather than both parents, which could be more aggressive or could tend to use more strikes than displays. Nests in the previous study were exposed to motorboat noise for 50% of the time between 6 am and 6 pm, with over 720 boat passes per day, whereas in the current study fish were exposed for 12% of this time period, with approximately 100 boat passes a day, due to the logistical restrictions of using real motorboats. The lower temporal intensity of this study could explain why no response was found in the striking behaviours.

Nedelec et al. (2017a) used loudspeakers to introduce motorboat-noise playback at natural nests; although the results of Simpson et al. (2016b) suggest that using such loudspeakers and recordings may be an effective experimental proxy for real motorboat noise, this is not supported here. The loudspeakers will not have accurately reproduced the acoustic composition of the real engine noise, and will have produced a directional cone of sound, so are less applicable to real-world hypotheses. The recordings used in the playback were from 2-stroke outboard motors, as opposed to the 4-stroke motors used in the current study. There is some emerging evidence that 2-stroke motors have a greater detrimental impact on marine life (Jain-Schlaepfer et al. 2018; McCormick et al. 2018), which perhaps explains the lack of response to noise exposure in overall striking behaviours in this experiment despite responses being found in the 2017 study.

Since noise-exposed parents were not changing how often they were striking potential larval predators, I conclude that noise-induced changes to the parental-care behaviours of *A. polyacanthus* were unlikely to be responsible for the increased larval mortality found in Nedelec et al. (2017a). An alternative explanation for the higher larval mortality at noise-exposed nests is that noise may directly compromise embryonic development. Fakan and McCormick (2019) found that playback of motorboat noise resulted in morphological differences and smaller yolks in *A. polyacanthus* eggs, although Bruintjes and Radford (2014) found no developmental effects of motorboat-noise playback on the eggs of daffodil cichlids. Another possibility is that changes in the behaviours of the predators may have made them more effective at capturing larvae, or that larval behaviours, for example escape responses, were affected (Simpson et al. 2016b).

The defensive behaviours studied here may not be exclusively related to parental care of the current clutch, but may also be related to territoriality and future reproductive opportunity. The presence of larvae increases the fitness stakes of accurate and effective defence, but there are additional risks. The cost of not responding as normal to intrusions during noise exposure may be high enough to counter the stress effects of noise: not only would the fish lose the current brood to

predation, the high-quality territory may be taken over by conspecifics (Hourigan 1986), affecting future reproductive opportunity. Furthermore, one or both adults could be predated: loss of one of the pair results in brood failure in this species (Nakazono 1993). Therefore, defence may be less susceptible to the effects of anthropogenic noise than other behaviours in *A. polyacanthus* due to the high fitness costs of ineffective territoriality.

The results from this study suggest that there would be minimal community- and ecosystem-level knock-on effects from breeding *A. polyacanthus* being exposed to noise from small motorboats, at least in relation to parental-care behaviours; other behaviours and physiological changes not measured here may be impacted by noise and subsequently have effects at these scales. This is certainly a reason to be optimistic, as highly territorial damselfish can influence the community structure and distribution of competitors on coral reefs (Robertson 1984; Bay et al. 2001; Ceccarelli et al. 2001; McCormick and Meekan 2007) and this family includes abundant omnivores and herbivores, so these species play a role in nutrient cycling (Wilkinson and Sammarco 1981). However, *A. polyacanthus* is unusual in caring for offspring at the juvenile stage (Bernardi 2011); the parental behaviours of other pomacentrids with similar ecosystem roles may be influenced by noise in different ways.

By experimentally introducing wild fish at natural nests to a real source of anthropogenic noise, this study has furthered our understanding beyond that achieved from previous research using tank-based and/or playback experiments. Although there is limited evidence here for an effect of motorboat noise on the territorial parental-care behaviours of larvae-guarding *A. polyacanthus*, this should not deter further research on these types of behaviours, particularly with regards to long-term sensitisation. The current study highlights the need for more repeated-exposure and chronic-exposure experiments in natural conditions, to gain a greater understanding of noise effects beyond initial short-term responses.

CHAPTER FOUR

General Discussion

This pair of studies presents field-based experimental evidence that exposure to motorboat noise causes potentially detrimental changes to parental-care behaviours in two common species of coral-reef fish. Male *Pomacentrus amboinensis* parents reduced egg tending (Chapter 2), which could lead to reduced hatching success of the brood. *Acanthochromis polyacanthus* parents of both sexes increased displaying to intruders, despite no increase in predator abundance around the nest (Chapter 3), which could represent unnecessary energy expenditure. Effects of noise on the parents during these vulnerable life-history stages could affect their reproductive success through impacts on the development or survival of the offspring, thereby influencing population and community dynamics.

The changes in egg tending found in *P. amboinensis* have a greater potential to influence offspring survival than the changes in the defensive behaviours of *A. polyacanthus,* as reduced fanning will certainly reduce oxygenation of the eggs in that moment, whereas inefficient territoriality may not result in any larval mortality for any given intrusion event. Therefore, embryos may be more vulnerable than larvae to indirect effects of motorboat-noise via parental behavioural changes. Different noise-induced changes to parental care relative to the developmental stage of the offspring have previously been found in the largemouth bass *Micropterus salmoides* (Maxwell et al. 2018). The susceptibility of egg tending to perturbation by noise in the present study is concerning, as parental care of eggs is common in pomacentrids so detrimental effects of motorboat-noise exposure on parental care, specifically on egg care, may be found in related species. Larval-guarding is extremely rare, found in only three species of pomacentrid (Bernardi 2011), therefore the responses to noise found in *A. polyacanthus* are less likely to be predictive of noise-effects on parental care in other members of the family. However, these defensive behaviours can also have a role in deterring predators of the adults and competitors for food and space across pomacentrid species (Thresher 1976; Brawley and Adey 1977; Robertson 1984). It is possible that motorboat noise may impact the defensive behaviours of other territorial pomacentrids outside of the context of parental care in a similar manner to parental *A. polyacanthus*.

Acanthochromis polyacanthus showed rapid recovery of baseline display rate after the end of short-term noise exposure, and apparent sensitisation over long-term repeated noise exposures, in contrast to the evidence of reduced responses found previously in other fishes (Bruintjes et al. 2016; Nedelec et al. 2016b; Radford et al. 2016; Holmes et al. 2017). It would be interesting to see if the short-term recovery found at the larval-care stage is also possible during the egg-care stage, both in *A. polyacanthus* and in other pomacentrids like *P. amboinensis,* despite the different parental behaviours exhibited between these life-history stages. Although *A. polyacanthus* sensitised to motorboat exposure in defensive display rate, the baseline rate of this behaviour was unaffected in the long term, and the striking behaviour of the parents was also largely unchanged. This, alongside

the short-term recovery to baseline behaviours, implies that many short-term exposures may be less impactful on parental care than continuous chronic noise, assuming that the maintained response over 15 min found in Chapter 3 continues over longer exposures. Further studies are required to determine the influence of chronic exposure in marine organisms on fitness-affecting behaviours such as parental care, as changing responses to continuous exposure may be possible, for example through habituation or increasing tolerance. Such experiments could also determine whether experience of one anthropogenic-noise source allows subsequent desensitisation to other sources (see also: Radford et al. 2016).

The current experiments used motorboats with 4-stroke outboard motors, which have been shown to have a lower impact on the physiology and behaviour of fish than 2-stroke engines (Jain-Schlaepfer et al. 2018; McCormick et al. 2018); these results are therefore relatively conservative estimates of the effects of motorboat noise on parental care. Further experiments should be conducted with treatments mimicking real-world activities, such as frequent motorboat passes (Ferrari et al. 2018). Such exposures would be more acoustically complex than the high-intensity, sudden-onset exposures used in Chapter 2; Chapter 3 demonstrates a more realistic motorboating regime. For example, there may be long, gradual lead-in and exit periods as the vessel approaches and leaves the area. Fish may be able to detect the noise from a great distance, so could be experiencing an extended period of stress, distraction, or masking, or could already be habituating or building tolerance to the exposure before it reaches peak intensity as the vessel passes. Additionally, noise from small recreational motorboats has commonly been used as an experimental stressor. Although motorboats are a common and ecologically-relevant noise source for fish, it would be beneficial to research the variation in effects on behaviour from other vessel types, since only a small number of studies have tested different noise sources on the same species (see: Picciulin et al. 2010; Shafiei Sabet et al. 2015; Radford et al. 2016; Spiga et al. 2017; Jain-Schlaepfer et al. 2018; McCormick et al. 2018).

Both studies presented here used real motorboats in natural conditions for the noise-exposure regimes (see also: Simpson et al. 2016b; Nedelec et al. 2017a; Jain-Schlaepfer et al. 2018; McCormick et al. 2018), as opposed to playback as has been common in the literature so far (see reviews: Kunc et al. 2016; Shannon et al. 2016). Playback of noise recordings does not accurately replicate the full spectra of noise directly from the source, and the physical properties of tanks modifies the sound further (Simpson et al. 2016b); it is difficult to apply the results from such experiments to natural scenarios (Shannon et al. 2016; Slabbekoorn 2016; Holmes et al. 2017). Tank-based experiments are valuable in describing effects in controlled conditions (Kunc et al. 2016), often at reduced cost compared to extensive fieldwork, and playback of noise recordings might be an effective proxy for investigating effects on fish (Simpson et al. 2016b, Ferrari et al. 2018). However,

these moves towards acoustic validity will give us a greater understanding of real-world consequences of noise exposure, and as such should provide valid evidence for policymakers to be used when designing mitigation strategies.

It is timely to design and implement solutions to mitigate the negative effects of marine noise pollution, for example temporal and spatial exclusion zones and speed limits near vulnerable habitats (McCloskey et al., in preparation). One potential mitigation strategy for motorboat-noise pollution emerging from this study is enforcement of restricted time-windows for motorboating; for example, if traffic is only allowed within a certain distance of a habitat for given time periods interspersed through the day. If implemented around habitats with noise-sensitive species, including pomacentrids, this could allow the fish to recover from short-term disturbance. Additionally, season-specific restrictions could be implemented to protect key species during the breeding season, in order to avoid impacts on parental-care behaviours. To the best of my knowledge, beyond the comparisons of engine types discussed above, there is no other experimental evidence of successful strategies to alleviate the impacts of motorboat noise on fish behaviour, and such questions should be addressed routinely in future research.

My thesis has addressed several key areas which, in combination, have not previously been researched in fish with regards to anthropogenic noise, investigating: (1) exposure of natural nests to real noise sources; (2) parental care, a vital set of fitness-affecting behaviours; (3) activities inside the nest as well as in the immediate territory; and (4) long-term repeated exposures. There are still many gaps in the literature regarding the fitness effects of anthropogenic noise on marine organisms. In relation to parental-care behaviours, future studies should quantify the impact of behavioural changes such as those found here on lifetime reproduction. Furthermore, exploration of the population, community and ecosystem consequences of changes to the behaviours of individuals will provide more comprehensive information for application in noise-reduction strategy development. Additionally, it is essential that experimental testing of realistic, affordable and effective noise-mitigation strategies, accessible to users and policymakers, is integrated into behavioural and physiological research in this field.

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Appendix

Table A.1: Taxonomic families identified as potential predators of *Acanthochromis polyacanthus* larvae, included in community counts as heterospecific piscivores (Chapter 3).

Family	English name(s)
Aulostomidae	Trumpetfishes
Belonidae	Needlefishes
Bothidae	Lefteye flounders
Carangidae	Trevallies
Cirrhitidae	Hawkfishes
Fistulariidae	Flutemouths
Holocentridae	Squirrelfishes; Soldierfishes
Lethrinidae	Emperors
Lutjanidae	Snappers
Mullidae	Goatfishes
Muraenidae	Moray eels
Nemipteridae	Coral breams
Platycephalidae	Flatheads
Plesiopidae	Longfins
Pomacentridae	Damselfishes
Pseudochromidae	Dottybacks
Rachycentridae	Cobias
Scorpaenidae	Scorpionfishes
Serranidae	Groupers; Anthias; Soapfishes
Sphyraenidae	Barracudas
Synodontidae	Lizardfishes
Terapontidae	Grunters
Tetraodontidae	Pufferfishes
Elasmobranchii (subclass)	Sharks and rays

Table A.2: Generalised linear mixed model (GLMMs) and linear mixed model (LMMs) summaries for Chapter 3 with age of larvae as a fixed effect. (a) Long-term exposure regime (baseline) (GLMMs), (b) introduction of short-term exposure (LMMs), (c) continuation of short-term exposure (LMMs), (d) post-short-term exposure (LMMs). n = number of observations. Random effect values show variance ± standard deviation (in italics). Fixed effect values show effect estimate ± standard error. GLMMs are presented with z-values, LMMs are presented with χ^2 values. Values are subject to rounding (3 d.p.).

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(a) Long-term exposure regime					
Display rate	55		48		
Treatment		0.311		0.756	0.132 ± 0.423
Larval age		0.921		0.357	0.039 ± 0.042
Interaction		-0.626		0.531	-0.038 ± 0.061
Intercept					-5.207 ± 0.312
Nest by site					*$4.76e^{-12}$ ± $2.18e^{-6}$*
Site					*0.000 ± 0.000*
Strike rate	55		48		
Treatment		-0.718		0.473	-0.412 ± 0.574
Larval age		-0.728		0.466	-0.032 ± 0.044
Interaction		-0.707		0.479	-0.048 ± 0.067
Intercept					-4.272 ± 0.406
Nest by site					*0.235 ± 0.485*
Site					*0.170 ± 0.412*
Strike rate proportion to conspecifics	40		34		
Treatment		-1.49		0.135	-2.115 ± 1.416
Larval age		-0.545		0.586	-0.059 ± 0.107
Interaction		1.88		0.061	0.381 ± 0.203
Intercept					-1.893 ± 0.815
Nest by site					*2.680 ± 1.637*
Site					*0.000 ± 0.000*
Strike rate proportion to heterospecific piscivores	39		33		
Treatment		0.515		0.607	0.405 ± 0.786
Larval age		-0.407		0.684	-0.030 ± 0.739
Interaction		0.197		0.844	0.028 ± 0.142
Intercept					1.517 ± 0.559
Nest by site					*$5.570e^{-1}$ ± 0.746*
Site					*$7.693e^{-7}$ ± 0.001*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(a) continued					
Count estimate conspecific	55		48		
Treatment		-1.351		0.177	-1.227 ± 0.909
Larval age		0.615		0.538	0.043 ± 0.070
Interaction		-0.801		0.423	-0.091 ± 0.113
Intercept					0.858 ± 0.604
Nest by site					*$5.515e^{-11}$ ± $7.426e^{-0.6}$*
Site					*$2.970e^{-1}$ ± $5.450e^{-1}$*
Count estimate heterospecific piscivore	55		48		
Treatment		-0.518		0.604	-0.221 ± 0.427
Larval age		-0.647		0.517	-0.021 ± 0.032
Interaction		-0.571		0.568	-0.026 ± 0.045
Intercept					2.756 ± 0.310
Nest by site					*$2.896e^{-10}$ ± $1.702e^{-5}$*
Site					*$1.301e^{-1}$ ± $3.607e^{-1}$*
Count estimate heterospecific non-piscivore	55		48		
Treatment		0.860		0.390	0.425 ± 0.494
Larval age		0.270		0.787	0.014 ± 0.051
Interaction		-1.528		0.127	-0.112 ± 0.073
Intercept					0.759 ± 0.368
Nest by site					*$8.589e^{-15-}$ ± $9.268e^{-8}$*
Site					*0.000 ± 0.000*
(b) Introduction of short-term exposure					
Display rate	55				
Treatment		0.661	1	0.416	-0.317 ± 0.242
Larval age		2.027	1	0.155	-0.029 ± 0.016
Interaction		1.437	1	0.230	0.026 ± 0.022
Intercept					0.284 ± 0.174
Nest by site					*0.000 ± 0.000*
Site					*0.054 ± 0.232*
Strike rate	54				
Treatment		0.048	1	0.827	-0.144 ± 0.193
Larval age		0.097	1	0.756	-0.011 ± 0.019
Interaction		1.212	1	0.271	0.030 ± 0.027
Intercept					0.089 ± 0.142
Nest by site					*0.000 ± 0.000*
Site					*0.003 ± 0.054*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(b) continued					
Strike rate to conspecifics	54				
Treatment		1.579	1	0.209	0.016 ± 0.062
Larval age		0.027	1	0.871	-0.003 ± 0.006
Interaction		0.301	1	0.583	0.005 ± 0.009
Intercept					-0.033 ± 0.045
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Strike rate to heterospecific piscivores	55				
Treatment		0.109	1	0.742	-0.096 ± 0.150
Larval age		0.174	1	0.677	-0.016 ± 0.015
Interaction		0.999	1	0.318	0.021 ± 0.021
Intercept					0.095 ± 0.110
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Strike rate to heterospecific non-piscivores	55				
Treatment		0.648	1	0.421	-0.178 ± 0.070
Larval age		0.367	1	0.544	-0.016 ± 0.007
Interaction		**6.666**	**1**	**0.010**	**0.025 ± 0.010**
Intercept					0.139 ± 0.052
Nest by site					*0.004 ± 0.062*
Site					*0.000 ± 0.000*
Count estimate conspecific	55				
Treatment		2.406	1	0.121	1.025 ± 1.118
Larval age		1.177	1	0.278	-0.082 ± 0.116
Interaction		0.002	1	0.961	-0.008 ± 0.160
Intercept					-0.513 ± 0.825
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Count estimate heterospecific piscivore	55				
Treatment		0.001	1	0.970	2.161 ± 3.506
Larval age		0.020	1	0.887	0.164 ± 0.237
Interaction		1.174	1	0.279	-0.352 ± 0.325
Intercept					0.643 ± 2.594
Nest by site					*59.500 ± 7.713*
Site					*0.000 ± 0.000*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(b) continued					
Count estimate heterospecific non-piscivore	55				
Treatment		0.280	1	0.597	-1.404 ± 1.016
Larval age		0.663	1	0.415	-0.097 ± 0.105
Interaction		**4.158**	**1**	**0.041**	**0.295 ± 0.145**
Intercept					0.411 ± 0.750
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
(c) Continuation of short-term exposure					
Display rate	53				
Treatment		1.323	1	0.250	-0.616 ± 0.314
Larval age		1.516	1	0.218	-0.057 ± 0.028
Interaction		2.605	1	0.107	0.062 ± 0.039
Intercept					0.521 ± 0.229
Nest by site					*0.000 ± 0.000*
Site					*0.034 ± 0.184*
Strike rate	53				
Treatment		0.205	1	0.651	0.209 ± 0.354
Larval age		1.576	1	0.209	-0.004 ± 0.036
Interaction		1.071	1	0.301	-0.051 ± 0.049
Intercept					0.167 ± 0.263
Nest by site					*0.030 ± 0.173*
Site					*0.000 ± 0.000*
(d) Post-short-term exposure					
Display rate	43				
Treatment		0.569	1	0.451	-0.403 ± 0.283
Larval age		0.395	1	0.530	-0.040 ± 0.030
Interaction		1.465	1	0.226	0.048 ± 0.040
Intercept					0.304 ± 0.212
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Strike rate	43				
Treatment		0.445	1	0.505	-0.263 ± 0.469
Larval age		0.467	1	0.494	-0.029 ± 0.049
Interaction		0.036	1	0.850	0.012 ± 0.064
Intercept					0.383 ± 0.352
Nest by site					*$1.187e^{-1}$ ± 0.345*
Site					*$2.004e^{-8}$ ± 0.000*

Table A.3: Generalised linear mixed model (GLMMs) and linear mixed model (LMMs) summaries for Chapter 3 with days of long-term exposure as a fixed effect. (a) Long-term exposure regime (baseline) (GLMMs), (b) introduction of short-term exposure (LMMs), (c) continuation of short-term exposure (LMMs), (d) post-short-term exposure (LMMs). W = Larval age window (1 = 1–4 days; 2 = 8–11 days). n = number of observations. Random effect values show variance ± standard deviation (in italics). Fixed effect values show effect estimate ± standard error. GLMMs are presented with z-values, LMMs are presented with χ^2 values. Values are subject to rounding (3 d.p.).

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(a) Long-term exposure regime					
Display rate	55		48		
Treatment		-0.107		0.915	-0.048 ± 0.453
Days of exposure		0.287		0.774	0.009 ± 0.032
Interaction		-0.150		0.881	-0.006 ± 0.039
Intercept					-5.056 ± 0.352
Nest by site					*$4.13e^{-12}$ ± $2.034e^{-6}$*
Site					*$6.917e^{-12}$ ± $2.630e^{-6}$*
Strike rate	55		48		
Treatment		-1.000		0.317	-0.579 ± 0.579
Days of exposure		0.848		0.397	0.028 ± 0.033
Interaction		0.168		0.866	0.007 ± 0.039
Intercept					-4.664 ± 0.416
Nest by site					*0.019 ± 0.138*
Site					*0.128 ± 0.358*
Strike rate proportion to conspecifics	40		34		
Treatment		0.899		0.369	-2.585 ± 1.586
Days of exposure		-1.630		0.103	0.061 ± 0.067
Interaction		1.768		0.077	0.156 ± 0.088
Intercept					-2.533 ± 0.910
Nest by site					*0.596 ± 0.779*
Site					*0.633 ± 0.796*
Strike rate proportion to heterospecific piscivores	39		33		
Treatment		0.351		0.725	0.671 ± 0.934
Days of exposure		0.719		0.472	0.020 ± 0.056
Interaction		-0.080		0.936	-0.007 ± 0.089
Intercept					1.156 ± 0.669
Nest by site					*$5.662e^{-1}$ ± $7.524e^{-1}$*
Site					*$3.405e^{-9}$ ± $5.836e^{-5}$*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(a) continued					
Count estimate conspecific	55		48		
Treatment		**-2.176**		**0.028**	**-1.851 ± 0.851**
Days of exposure		0.962		0.336	0.048 ± 0.048
Interaction		0.074		0.941	0.004 ± 0.058
Intercept					0.676 ± 0.596
Nest by site					*$2.063e^{-11}$ ± $4.542e^{-6}$*
Site					*$2.020e^{-1}$ ± $4.494e^{-6}$*
Count estimate heterospecific piscivore	55		48		
Treatment		-1.569		0.117	-0.684 ± 0.436
Days of exposure		-0.258		0.797	-0.005 ± 0.020
Interaction		1.202		0.230	0.031 ± 0.026
Intercept					2.683 ± 0.315
Nest by site					*$5.055e^{-10}$ ± $2.248e^{-5}$*
Site					*$1.424e^{-1}$ ± $3.774e^{-1}$*
Count estimate heterospecific non-piscivore	55		48		
Treatment		-0.030		0.976	-0.015 ± 0.492
Days of exposure		0.988		0.323	0.030 ± 0.030
Interaction		-0.340		0.734	-0.013 ± 0.039
Intercept					5.335 ± 0.371
Nest by site					*$1.413e^{-14}$ ± $1.189e^{-7}$*
Site					*$5.337e^{-12}$ ± $2.310e^{-6}$*
(b) Introduction of short-term exposure					
Display rate	55				
Treatment		0.680	1	0.410	-0.451 ± 0.240
Days of exposure		0.034	1	0.855	-0.020 ± 0.010
Interaction		**4.955**	**1**	**0.026**	**0.030 ± 0.013**
Intercept					0.297 ± 0.175
Nest by site					*0.000 ± 0.000*
Site					*0.052 ± 0.227*
Strike rate	54				
Treatment		0.046	1	0.831	0.136 ± 0.204
Days of exposure		0.260	1	0.610	0.002 ± 0.013
Interaction		0.437	1	0.509	-0.012 ± 0.018
Intercept					0.003 ± 0.151
Nest by site					*$1.007e^{-9}$ ± $3.174e^{-5}$*
Site					*$2.303e^{-3}$ ± $4.799e^{-6}$*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(b) continued					
Strike rate to conspecifics	54				
Treatment		1.567	1	0.211	0.049 ± 0.065
Days of exposure		0.161	1	0.689	-0.001 ± 0.004
Interaction		0.008	1	0.930	0.001 ± 0.006
Intercept					-0.044 ± 0.049
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Strike rate to heterospecific piscivores	55				
Treatment		0.107	1	0.744	0.070 ± 0.156
Days of exposure		0.093	1	0.761	0.005 ± 0.011
Interaction		0.104	1	0.747	-0.004 ± 0.013
Intercept					-0.042 ± 0.119
Nest by site					*$4.225e^{-16}$ ± $2.055e^{-8}$*
Site					*0.000 ± 0.000*
Strike rate to heterospecific non-piscivores (W1)	27				
Treatment		1.592	1	0.207	-0.333 ± 0.115
Days of exposure		3.048	1	0.081	-0.035 ± 0.009
Interaction		**12.481**	**1**	**<0.001**	**0.036 ± 0.010**
Intercept					0.314 ± 0.086
Site					*0.011 ± 0.103*
Strike rate to heterospecific non-piscivores (W2)	28				
Treatment		2.010	1	0.147	-0.042 ± 0.130
Days of exposure		0.237	1	0.627	-0.006 ± 0.007
Interaction		0.738	1	0.390	0.008 ± 0.009
Intercept					0.059 ± 0.093
Site					*0.000 ± 0.000*
Count estimate conspecific	55				
Treatment		2.673	1	0.102	0.984 ± 1.145
Days of exposure		2.302	1	0.129	-0.075 ± 0.077
Interaction		0.002	1	0.968	0.004 ± 0.098
Intercept					-0.274 ± 0.872
Nest by site					*$4.188e^{-15}$ ± $6.471e^{-8}$*
Site					*0.000 ± 0.000*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(b) continued					
Count estimate heterospecific piscivore	55				
Treatment		0.001	1	0.971	0.020 ± 4.162
Days of exposure		0.169	1	0.681	0.053 ± 0.213
Interaction		0.001	1	0.975	0.009 ± 0.284
Intercept					1.081 ± 3.086
Nest by site					*6.129e ± 7.829*
Site					*$1.890e^{-5}$ ± 0.004*
Count estimate heterospecific non-piscivore (W1)	27				
Treatment		1.183	1	0.277	-0.261 ± 1.195
Days of exposure		1.185	1	0.276	0.147 ± 0.131
Interaction		0.469	1	0.493	-0.102 ± 0.149
Intercept					-0.584 ± 0.951
Site					0.000 ± 0.000
Count estimate heterospecific non-piscivore (W2)	28				
Treatment		2.425	1	0.119	2.852 ± 2.516
Days of exposure		1.917	1	0.166	-0.065 ± 0.129
Interaction		0.423	1	0.516	-0.118 ± 0.181
Intercept					0.327 ± 1.813
Site					*0.000 ± 0.000*
(c) Continuation of short-term exposure					
Display rate	53				
Treatment		1.454	1	0.228	-0.289 ± 0.326
Days of exposure		0.823	1	0.364	-0.014 ± 0.020
Interaction		0.021	1	0.884	0.004 ± 0.026
Intercept					0.316 ± 0.244
Nest by site					*$5.017e^{-11}$* ± $7.083e^{-6}$
Site					*$2.815e^{-1}$* ± $5.686e^{-1}$
Strike rate	53				
Treatment		0.163	1	0.687	0.336 ± 0.379
Days of exposure		0.016	1	0.901	0.026 ± 0.025
Interaction		1.723	1	0.189	-0.043 ± 0.033
Intercept					-0.116 ± 0.287
Nest by site					*0.034 ± 0.186*
Site					*0.000 ± 0.000*

Fixed effect	n	z-value/χ^2	df	p	Effect ± SE
(d) Post-short-term exposure					
Display rate	43				
Treatment		0.623	1	0.430	-0.347 ± 0.328
Days of exposure		0.001	1	0.973	-0.017 ± 0.027
Interaction		0.580	1	0.447	0.024 ± 0.032
Intercept					0.230 ± 0.267
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*
Strike rate	43				
Treatment		0.300	1	0.584	-0.255 ± 0.497
Days of exposure		**8.010**	**1**	**0.005**	**-0.070 ± 0.041**
Interaction		0.073	1	0.787	0.013 ± 0.048
Intercept					0.821 ± 0.405
Nest by site					*0.000 ± 0.000*
Site					*0.000 ± 0.000*